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THIS VOLUME OF

THE JOURNAL OF COMPARATIVE NEUROLOGY

IS DEDICATED TO

PROFESSOR LUDWIG EDINGER

ON HIS SIXTIETH BIRTHDAY, APRIL 13th, 1915

IN COMMEMORATION OF HIS FUNDAMENTAL RESEARCHES IN

COMPARATIVE NEUROLOGY

TO THE INSIGHT AND INDUSTRY OF EDINGER WE OWE THE FIRST COMPREHENSIVE DEMONSTRATION OF THE VALUE OF THE COMPARATIVE METHOD IN NEUROLOGY, AS EXEMPLIFIED IN HIS VOLUMINOUS RESEARCHES AND IN THE SUCCESSIVE EDITIONS OF HIS "VORLESUNGEN" FROM 1885 TO THE PRESENT TIME. THE GUIDING PRINCIPLES OF THESE RESEARCHES HE FORMULATED EARLY IN HIS CAREER IN THESE WORDS:

ES muss eine Anzahl anatomischer Anordnungen geben, die bei allen Wirbelthieren in gleicher Weise vorhanden sind, diejenigen, welche die einfachsten Aeusserungen der Thätigkeit des Centralorgans ermöglichen. Es gilt nur immer dasjenige Thier oder diejenige Entwicklungsstufe irgend eines Thieres ausfindig zu machen, bei der dieser oder jeniger Mechanismus so einfach zu Tage tritt, dass er voll verstanden werden kann. Hat man das Verhalten einer solchen Einrichtung, eines Faserzuges, einer Zellanordnung, nur einmal irgendwo ganz sichergestellt, so findet man sie gewöhnlich leicht auch da wieder, wo sie durch neu Hinzugekommenes mehr oder weniger undeutlich gemacht wird. Das Auffinden solcher Grundlinien des Hirnbaues aber scheint die nächstliegende und wichtigste Aufgabe der Hirnanatomie. Kennen wir nur erst einmal sie, so wird es leichter sein, die complicirten Einrichtungen zu verstehen, mit denen das höher organisirte Gehirn arbeitet.

THE CENTRAL RELATIONS OF THE CRANIAL NERVES IN SILURUS GLANIS AND MORMYRUS CASCHIVE

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TWENTY-ONE FIGURES

The following researches were started with the idea of studying the topography of the motor nuclei in the brain of Silurus glanis, since a description of these nuclei in the central nervous system of siluroid fishes has not yet been given and we may expect interesting relations in this connection on account of the enormous development of special sensory systems and their secondary connections.[1]

It is known that the siluroids[2]—including also the European representative of that order, Silurus glanis[3]—are distinguished by an extraordinary development of the sense of taste, the receptive organs of which are distributed over the head and the body and are innervated by the ramus recurrens facialis, which is very large in these animals. This has been demonstrated, among others, by Herrick for Ameiurus melas, and our photograph (fig. 1A), taken from an anatomical preparation made by Mr. Schepman, shows the same for Silurus glanis.

It was to be expected that the preëminence of one set of sensory impressions should have a pronounced influence on the structure of the central nervous system, which would also appear

[1] The olfactory and optic nerves are not discussed here because it was chiefly the medulla oblongata and basis mesencephali which interested me.

[2] C. J. Herrick, The central gustatory paths in the brains of bony fishes. Jour. Comp. Neur., vol. 15, 1905, p. 375. The organ and sense of taste in fishes. Bul. U. S. Fish Commission for 1902, pp. 237–272, Washington, 1904. The cranial nerves and cutaneous sense organs of the North American siluroid fishes. Jour. Comp. Neur., vol. 11, 1901, p. 177.

[3] F. Merkel, Ueber die Endigungen der sensiblen Nerven in der Haut der Wirbelthiere. Rostock, 1880.

in the arrangement of the motor nuclei. The results justify this expectation, as appears from the topographic diagrams appended to this paper (fig. 21).

The arrangement is characteristic of a 'taste fish,' and shows this character in a very pronounced way. I have thought it necessary to give also a description of the sensory roots and their connections, first because such a description, though given in Herrick's paper for the North American forms, has not yet been given for the European representative of the siluroids, and second, because a knowledge of the sensory roots, centers and secondary paths is absolutely necessary for the understanding of the topography of the motor nuclei. Herrick's excellent description of Ameiurus has been a valuable guide to me, the more so since I had a complete series of Ameiurus nebulosus at my disposal.

After having finished my work on Silurus, it seemed interesting to me to examine another fish, whose physiological characteristics were very different from those of Silurus. I chose Mormyrus caschive, whose motor nuclei have not yet been described and which is, moreover, an interesting object on account of the enormous development of the lateralis nerves and valvula cerebelli. The study of the latter has also enabled me to correct some statements occurring in the literature concerning this peculiar brain.

The Central Institute for Brain Research in Amsterdam has put at my disposal series of sections through the brains of Silurus glanis and Mormyrus caschive. The objects, embedded in celloidin, were cut into sections of 25 micra and alternately stained after van Gieson and Weigert-Pal. The Weigert-Pal series was counterstained with paracarmine.

My projections have been made after the van Gieson series. In order to get the most exact reconstruction of the topographic positions of the motor nuclei and roots, I projected them on the sagittal plane lying medially in the raphé in the following way. In each section the distance from the ventral border of the bulb to the floor of the fourth ventricle was measured with an ocular

micrometer. If the most ventral part of the bulb was not in the region of the raphé, it was projected on the sagittal plane of the raphé. The micrometer being put parallel with the raphé, a movement of the object table perpendicularly to the micrometer was sufficient to project the point in question on the medial plane. At the dorsal limit of the bulb the first curve toward the horizontal in the lining of the ventricle was registered. In the same way the ventral and dorsal limits of each nucleus were registered and projected on the medial plane.

In my projections each section was counted as 2 mm. Since each section was 25 micra thick and the series contained only alternating sections, these 2 mm. represent 50 micra, thus giving an enlargement of 40 diameters. The same magnification was applied to the dorso-ventral dimensions, which likewise gave the natural relations forty times enlarged.

Since my projections have been four times reduced for reproduction, the figures represent the natural relations ten times magnified and projected on the sagittal plane through the raphé. The ventral border of the medulla has been taken as a horizontal line. It is actually slightly curved, but the curve of the oblongata in teleosts is generally so insignificant that the error hereby introduced has only a slight influence on the exact relations.

Figure 2 shows the projected points connected by lines. The dotted line represents the floor of the ventricle, or rather, since the ventral border of the bulb is drawn straight, it represents the algebraic addition of the curves occurring in the floor of the ventricle and those in the ventral border of the bulb.

The limits of the nuclei are indicated by full lines, in doubtful cases by dashes alternating with dots. Local interruptions in the nuclei are indicated by curved lines. Beneath the base line, representing the ventral border of the bulb reduced to a horizontal line, the levels of entrance of the motor roots are registered, thus enabling us to see the distances between the roots and the spaces occcupied by their entrance.

Figure 3 is based on figure 2 and is designed to give a simpler view of the relations, the curves being smoothed by the omission

of small irregularities. In order to indicate to which nuclei the roots correspond, the same markings are used as in Kappers' diagrams.

In figure 4 the exact place of entrance—not merely the level—of each root is projected, together with its central course. Of the latter, only the most important points were projected, these being connected by rather smooth lines.

These three projections are intended to show the natural forms and positions of the nuclei and roots in the medulla and basis mesencephali in the most painstaking way. The differences between these projections and Kappers' diagrams lie chiefly in the fact that Kappers draws each nucleus as it appears when projected on its own radial, the center of the radius being the middle of the bottom of the IVth ventricle, whereas I projected all the nuclei on the medial plane of the raphé. From this it results that the place of the V and VII nuclei is less ventral in my projection than in Kappers' diagram. Moreover, Kappers does not aim to show the exact form of the nuclei, but only the spaces within which they are found.

SILURUS GLÄNIS

The eye-muscle nerves in Silurus are poorly developed, in conformity with the life habits of this animal which belongs to the bottom-feeders, living in the mud and searching for their food chiefly by exploring the bottom with their taste organs. This is in contrast to the plankton feeders, which swim around near the surface and seek their food chiefly with their visual apparatus.

The *oculomotor nerve* is, consequently, relatively thin. Approaching the mesencephalon in the cleft between the inferior lobes and the base of the midbrain, it pierces through the base in a caudo-frontal direction (fig. 4). As figure 2 shows, the nucleus lies several sections in front of the entrance of the root, its caudal part being the larger. The cells are located near the raphé, but it is not an unpaired nucleus in the strict sense, since there is clearly a small region devoid of cells between the left and the right nucleus. The dorso-ventral and transverse diameters of

the nucleus are approximately the same, but in the caudal part the transverse dimension may be a trifle smaller. Directly behind the third nerve a considerable decussation of cerebellar fibers is found, as is the case in most teleosts.

The *trochlearis* enters the brain near the transition from the tectum opticum to the cerebellum. Its fibers are not as thick as those of the III nerve. After having entered the brain, they first run in a medio-dorsal direction, bending slightly caudad.

It is extremely difficult to trace the IV root in the intricate net-work of fiber systems found in this level of the brain and it may be that its course as indicated in my projection (fig. 4) needs correction. Its entrance, however, as well as the location of the nucleus, are not in doubt.

The IV nucleus has a relatively lateral position under the floor of the ventricle and it is not connected with the III nucleus. This separation of the III and IV nuclei occurs often in teleosts, but is not a constant feature.

Very striking in Silurus is the very frontal place of entrance of the IV root (fig. 4). In all the bony fishes as yet examined this root enters the brain on a level behind the nucleus (Tinca, Cottus, Pleuronectidae, Gadus, Lophius).[4] Only once, in a holocephalic fish, Chimaera,[5] has such a frontal entrance of the IV root been found, its fibers here leaving the brain on a level with the oculomotor nucleus. This frontal displacement of the trochlearis entrance is most probably due to mechanical factors only.

The *trigeminus root* in Silurus (fig. 5) is intimately connected at its entrance with the sensory VII root and the anterior lateralis root, as has already been observed by Stannius.[6] Similar conditions are described by C. J. Herrick[7] in the North American siluroid fishes. Nevertheless, the motor and sensory V can be

[4] Kappers, Weitere Mitteilungen über Neurobiotaxis. No. VII. Folia Neurobiologica, Sommer-Ergänzungsheft, Bd. 6, 1912, figs. 24, 25, 29, 33, 34.

[5] Kappers, Motor nuclei in the oblongata and midbrain of Chimaera monstrosa. Proc. kon. Akad. van Wetenschapp., Amsterdam, March 8, 1912, p. 1141.

[6] Stannius, Das periferische Nervensystem der Fische. Rostock, 1849, p. 21.

[7] C. J. Herrick, The cranial nerves and cutaneous sense organs of the North American siluroid fishes. Jour. Comp. Neur., vol. 11, p. 183. This author also observes that the gasserian ganglion and ganglion geniculi are fused.

easily distinguished from the sensory VII and nervus lateralis anterior by reason of the character of their fibers. The sequence of the different components of this root complex near its entrance is such that, in a transverse section, the motor V forms the most medial and ventral part of the complex. Next comes the sensory V, then the sensory VII, and most dorsal the nervus lateralis anterior. These roots shift gradually into the brain stem.

The intramedullary course of the motor V is nearly horizontal and inclined in a caudal direction. Near the frontal pole of its nucleus it curves inward around the anterior secondary gustatory tract (fig. 6), and thus reaches its motor cells. The fibers—which are coarse and easily distinguished from the surrounding tracts—clearly form two bundles, a frontal one arising from the frontal pole of the nucleus and a caudal one originating in its caudal part. I have not been able to decide whether these bundles remain thus separated during their further course or whether they again mingle. The motor nucleus has an extremely ventral position (figs. 6 and 21), just mesially of the entrance of the motor VII root. The cells are large and have considerable dendritic outgrowths. Their position is entirely under and near the anterior secondary gustatory tract (fig. 6). In some places they form cellular columns which lie embedded among the associational systems.

The motor V nucleus grows considerably smaller at about the middle of its length, thus exhibiting an isthmus which connects the two parts. A complete separation does not occur, though a division is thus clearly indicated. Such an arrangement of the motor V nucleus in two divisions has also been described in Tinca, which by the ventral position of the V nucleus (fig. 21) likewise exhibits a striking resemblance to Silurus. Both animals are characterized by a considerable development of the organs of taste.

As was stated above, the sensory V[8] has a position lateral to the corresponding motor root outside the medulla (fig. 5). Where the motor V curves around the anterior secondary gustatory

[8] The mesencephalic root of the V nerve could not be traced with certainty.

tract it is closely followed by the sensory root, which remains dorsally of these gustatory fibers (figs. 6, 7 and 8).

More caudally—behind the place where the secondary fibers from the sensory VII nucleus that constitute the larger part of the anterior secondary gustatory tract have disappeared from the sections—the descending sensory V acquires a more medial position, but only for a short distance, because it is soon pushed more laterally again, and especially more dorsally (fig. 10), by the communis nucleus of the IX and X.[9]

In the region of the X the descending V receives a considerable bundle of root fibers from the second sensory X root, which are doubtless the somatic sensory fibers of that nerve which have been described by C. J. Herrick.

Where the oblongata passes over into the spinal cord, the descending V gradually disappears in the posterior horn of the cervical gray, which thus constitutes a correlation center for the sensibility of the skin of the head and the front part of the body.

The *motor VII root* (figs. 4 and 6) directly after its entrance passes through the anterior secondary gustatory tract (fig. 7) as a strong coarse fibered tract, runs to the floor of the fourth ventricle through some strong bundles of the fibrae arcuatae internae, curves in a caudal direction (frontal knee-bend), and proceeds backward in a horizontal course laterally from the fasciculus longitudinalis posterior and Mauthner's fiber (fig. 8). Directly behind the frontal pole of the VII nucleus its fibers descend and diverge as indicated in figures 4 and 8.

It is very interesting that a more caudal course of motor VII fibers (fig. 4) to the dorsal cell column of the IX and X, as occurs in most teleosts, cannot be traced in Silurus.

This absence of a caudal VII root is the more interesting since in Tinca this caudal root is already considerably diminished in comparison with the Pleuronectidae (Hippoglossus, Rhombus, Pleuronectes). The same process of frontal, and especially ventral migration of the motor VII cells to the region of the

[9] It seems strange to me that, while the sensory V has a relatively more ventral position in Mormyrus than in Silurus, the sensory communis roots in Silurus run dorsal to that tract while in Mormyrus they run ventrally of it.

anterior secondary gustatory tract (fig. 8), already so conspicuous in Tinca, is thus completed in Silurus. This, however, should not astonish us, since also in the position of the motor V nucleus (fig. 6) the predominating influence of this gustatory system and its direct surroundings on the position of the motor cells is so strikingly exhibited.

In Silurus the descending branch of the motor VII is split up into two parts by dorsal arcuate fibers (see fig. 4) and a comparison with the Pleuronectidae and other bony fishes reveals that that part of the descending branch of the VII which descends behind the dorsal commissure contains the fibers which in other teleosts proceed to the dorsal column of the motor X nucleus.

The frontal part of the VII nucleus contains, just as in Tinca, some more dorsally located cells (fig. 2). The greater part of the motor VII nucleus lies, however, in the line continuing the V nucleus (fig. 8), forming one interrupted column with it, both influenced in their position by the anterior secondary gustatory tract and spinal V tract. This forms a great contrast with the position found in Mormyrus, where the facial nucleus—on account of the slight development of the anterior gustatory tract—has kept its more primitive dorsal position near the floor of the fourth ventricle (fig. 21).

The *sensory VII root* is a predominating feature in the structure of the oblongata of this fish. The hypertrophy of this root, as already stated above, is chiefly due to the enormous development of its recurrent branch, which supplies the taste organs of the head and of the whole body with sensory fibers.[10] The large size of this root, and especially of its ramus recurrens, has already been observed by Stannius (*loc. cit.*, p. 51). In figure 1 I give a photograph of its anatomical relations from a preparation made by Mr. Schepman.

As I have already said, Herrick has stated the same for North American siluroid fishes (Jour. Comp. Neur., vol. 15, 1905, p. 378). The taste buds on the skin of Silurus, as previously

[10] Regarding the older and erroneous views about the ramus recurrens VII, see M. Juge, Recherches sur les nerfs cérébraux et la musculature céphalique du Silurus glanis L. Revue suisse de zoologie, T. 6, fasc. 1, Geneva, 1899, p. 91.

described by Merkel (*loc. cit.*, supra, p. 74), can be seen with the naked eye, by reason of their surrounding pigment, over the whole body and even the tail.

Near the periphery of the oblongata the sensory VII lies laterally of the sensory V (fig. 5), and is easily distinguished from it by the finer caliber of its fibers. This big root gradually shifts into the bulb. Running in a medial direction over the descending V (fig. 6), it is separated from the latter by some very coarse fibers of the nervus vestibularis (fig. 7). It can be easily observed how the sensory VII is pushed aside on its way to the lobus sensibilis VII by the enormous development of the lobus lineae lateralis (Johnston) (fig. 7). More caudally the lobus lineae lateralis is pushed dorsad and laterad, where the sensory VII enters the big lobus sensibilis VII (fig. 8).

The mode of termination of the sensory VII root in the lobus sensibilis VII is repeated in the case of the sensory IX and X nerves, so that I wish to describe it in a little more detail.

As soon as the sensory VII has reached the lobus sensibilis VII, it sends a considerable part of its fibers to form a dorso-lateral capsule of the lobe. The capsular, or peripheral, fibers are of especial importance to us, because, as Herrick has first observed, their number is increased in those fishes which possess a larger number of taste buds (consequently they are further enormously increased in the sensory X nucleus of cyprinoid fishes where the palatal organ has so many taste buds).

Besides this capsular root, the sensory facialis has two other roots, of which one pierces into the center of the lobus (fig. 8, *centr.f. VII*) and the second proceeds in a medial direction beneath it, crossing the fibers of the secondary gustatory tract, then running some distance backward near the lateral wall of the fourth ventricle. These fibers, as well as a part of the central fibers of the sensory VII, descend a considerable distance (fig. 9, *m. VII. f.*), so that the prevagal part of the fasciculus solitarius is well developed in Silurus and does not disappear until the level of entrance of the IX nerve.

Since, apart from the capsular taste fibers, the facialis contains also general tactile fibers for the mucous lining of the mouth,

the totality of its center is called the communis gray, which expression means that it is in general difficult, if not entirely impossible, to separate the two sorts of fibers in it (see, however, below).

From this lobus facialis, especially from its dorso-medial periphery where a great many of the capsular fibers end, a great number of secondary fibers arise (figs. 8 and 9), constituting the anterior secondary gustatory tract already often mentioned. This tract is located near the descending V and runs chiefly, if not entirely, in a frontal direction following the spinal V tract, and ascending, when the latter has left the bulb, in a fronto-dorsal direction to the so-called Rindenknoten (Mayser), or anterior secondary gustatory nucleus.

Apart from these fibers, Herrick has described descending gustatory fibers which do not originate from the dorso-medial periphery of the lobus VII but from the lateral part and descend along the spinal V tract. I do not doubt the existence of this bundle in Silurus, but have not been able to trace it from its origin. The fact that an area of fibers resembling in aspect and position those of the anterior gustatory tract continues also backward to the more caudal levels of the oblongata, even beyond the calamus, speaks in favor of their presence also in my object.

Although the gustatory character of these two systems cannot be proved with exactness, there is much in favor of the names applied by Herrick, because these fibers originate from the peripheral part of the lobus, in which are the terminals of the capsular fibers whose numbers are augmented, as stated above, when the number of taste buds is increased. Another reason is that these tracts themselves augment with the multiplication of taste buds.

These tracts, or rather the correlative gray matter which accompanies them, determine the position of the motor V and VII nuclei, which acquire a ventral position where these tracts are highly developed, as in cyprinoids and siluroids, and remain more dorsal where these systems are poorly developed, only sending dendrites in their direction. Since in cyprinoids (Tinca) and siluroids these gustatory systems are enormously increased,

it is not strange to find the same position of the motor V and VII nuclei in both.

Concerning the *abducens nucleus* not much can be said. The III and IV nuclei and roots themselves being small, the VI root is hardly recognizable.

Whilst in all teleosts as yet examined two VI roots and two VI nuclei could be detected, I could find only one small root in my object, at the level of the posterior rootlet in other teleosts. The corresponding cells have a rather ventral position but cannot be easily delimited from the surrounding reticular cells. The second (probably more frontal) root and nucleus could not be found, perhaps because the ventral border of the bulb was somewhat damaged on more frontal levels.

The *motor glossopharyngeus root* has the typical course found in teleosts. It enters slightly frontally and ventrally from the level of the corresponding sensory root, and runs in a frontal direction near the base of the bulb, bordering the facial nucleus (figs. 4 and 9). At the frontal level of that nucleus it turns in a dorsomesial direction, acquires a position near the fasciculus longitudinalis posterior, and can be traced backward again along that tract until it reaches its place of origin in the frontal pole of the dorsal IX + X nucleus. The sinuous course of this root thus corresponds with the course described by Mayser[11] in the cyprinoids, by C. J. Herrick[12] in Menidia, and recently by Kappers[13] in several other teleosts.

The *sensory glossopharyngeus root* enters the brain at the same level as the nervus lateralis posterior, from which it is distinguished by the finer caliber of its fibers (fig. 10). In the oblongata the course of the root is fronto-dorsal for a short distance (proceeding not nearly so far frontally as the corresponding motor root).

[11] Mayser, Vergleichend-anatomische Studien über das Gehirn der Knochenfische mit besonderer Berücksichtigung der Cyprinoïden. Zeits. f. Wissensch. Zool., Bd. 36, 1881, p. 303.

[12] C. J. Herrick, The cranial and first spinal nerves of Menidia. Jour. Comp. Neur., vol. 9, 1899, p. 250.

[13] Kappers, Weitere Mitteilungen über Neurobiotaxis. No. VII. Ueber den motorischen Glossopharyngeus und Facialis bei niederen Vertebraten. Folia Neurobiologica, Bd. 7, 1914, p. 383.

This root, like the sensory VII root, appears to end by three branches. A relatively small number of fibers constitutes the dorso-lateral capsule of the glossopharyngeal lobe (fig. 10, *d.c.l. IX*). The other two branches contain respectively finer fibers and fibers of a somewhat larger caliber.

The thinnest fibers (fig. 10, *s. IX, th.*), provided with slender myelin sheaths, have the most caudal position in the concavity which the root forms while curving around the spinal V tract. Entering the communis gray, they terminate in its center and in the dorso-medial periphery of the lobus glossopharyngeus.

The thicker fibers separate from the common sensory stem when this has reached the dorsal border of the spinal V tract. Instead of running in a dorsal direction as the other fibers do, they run mesad (fig. 10, *s. IX, th. m.*) and—like the corresponding fibers of the sensory VII—they cross the bundles of the secondary gustatory tract, passing through or beneath the communis gray. Having reached a more mesial position, they successively split up in the communis gray. Some of them, however, join the descending facial fibers and like them descend for a short distance, thus contributing to the formation of the prevagal fasciculus solitarius.

Of the sensory glossopharyngeal fibers mentioned above, those which end in the dorsal periphery of the lobus intermingle intimately with sensory vagus fibers of the same character, which proceed a short distance frontally to join this system. From the dorso-medial part of the sensory IX lobe secondary gustatory fibers also arise (fig. 10) and ascend along the spinal V tract, joining the same system from the facial lobe, but not in so large numbers as those, the sensory IX lobe being much smaller than the sensory VII nucleus because it innervates taste buds of the mucous lining of the pharynx and first posthyomandibular gills only.

Descending gustatory fibers are not so easily demonstrated. Herrick also mentions that the descending fibers are much less conspicuous and that they do not arise from the dorso-medial but from the dorso-lateral periphery of the lobe. Apart from this system, fibers should be mentioned which also arise from the lateral

part of the lobe—not from the dorso-medial part—and cross the dorsal part of the raphé. It is difficult to trace them separately because they mingle with or are covered by dorsal arcuate fibers from the tuberculum acusticum. There are not very many of these fibers, but their presence is easily demonstrable. Herrick considers them as reflex fibers for the cervical cord, which is probable on account of their position in or next to the highway of motor reflex fibers, the fasciculus longitudinalis posterior.[14]

The *motor roots of the vagus* enter the brain some distance in front of the sensory roots, as was also the case with the motor IX. Their place of entrance is also more ventral. This separation is more conspicuous in the frontal vagus root than in the more caudal roots.

The motor roots run in a fronto-medial direction, their nucleus being located dorsally near the floor of the fourth ventricle (fig. 4). In the frontal extremity of the nucleus some of the cells exhibit a tendency to shift in a ventral direction (fig. 10). In more caudal levels the nucleus acquires a more dorsal position.

The column is divided into some smaller cell groups fairly well separated from each other. In most cases each of these groups corresponds with a rootlet (fig. 4). Outside the brain stem the rootlets join and leave the bulb as one trunk. The frontal rootlets of the motor X run under or through the secondary gustatory tract, the caudal rootlets over it leaving the brain at a more dorsal level.

The *sensory vagus* has two roots, of which only the caudal one contains somatic fibers that join the descending V root. The rest of the sensory X contains also two sorts of fibers,[15] just like the sensory IX. The thinner fibers provided with small

[14] C. J. Herrick. These fibers are considerably hypertrophied in the codfish and probably have an influence on the movement of the pectoral fins, which in this animal are important instruments for taste exploration. Compare C. J. Herrick. A study of the vagal lobes and funicular nuclei of the brain of the codfish. Jour. Comp. Neur., vol. 17, 1907, p. 67.

[15] When dealing with the sensory VII and sensory IX, I mentioned also capsular fibers. These are not absent in the vagus, but seem to be connected with the dorso-medial system which probably also serves gustatory impulses. The medial branch represents Herrick's 'deep root' of the communis nerves, if I understand him well.

myelin sheaths do not descend, but ascend, obliquely and, running in a fronto-dorsal direction, join the dorsal endings of the IX, as already stated above. The other somewhat thicker and more heavily myelinated visceral sensory fibers also ascend for a short distance, turn again mesad over the spinal V tract, and then end, descending near the lateral wall of the ventricle. Although these fibers descend for a short distance, the visceral sensory root of the vagus does not form a real tractus solitarius, as occurs in reptiles, birds and mammals.

The positions of the different constituents of the visceral sensory X roots are such that the better myelinated fibers (the mesial root) lie ventro-medial to the poorly myelinated dorsal root fibers. They do not leave the brain directly, but run along the lateral border inside the brain for some distance and join other vagus fibers. The different constituents of these roots can still be distinguished after the roots have left the brain. The same process is repeated in the successive caudal roots, and also the position of the poorly myelinated dorsal fibers—lateral from the better myelinated mesial fibers—is repeated in the posterior levels of the bulb.

More caudally the poorly myelinated fibers not only leave the gray substance by curving dorsally around the lobus X, but they also leave it directly. This process is followed (perhaps it is the consequence of it) by a course of the poorly myelinated fibers through the spinal V tract instead of dorsally of it.

Concerning the somatic sensory fibers of the second vagal root, it may be mentioned that they form a dorsal part of the sensory root near its entrance. When entering the brain they are at first still separated from the descending V by the visceral sensory fibers; but as soon as these disappear from the sections they closely join the descending V, with which they can be traced to the posterior horn of the cervical cord.

It is known that in Petromyzon (Johnston[16]) and in primitive sharks (Kappers[17]) somatic sensory fibers occur in the VII and

[16] Johnston, The nerve components of Petromyzonts. Morph. Jahrb., Bd. 34, 1905. The nervous system of vertebrates. Philadelphia, 1906, p. 107 and fig. 50.

[17] Kappers, Der Geschmack, perifer und central. Psychiatrische en Neurologische Bladen, Nos. 1 and 2, 1914, fig. 3, pp. 102 and 103.

IX and also join the spinal V tract—a striking example of functional arrangement of fiber systems on account of their correlated function.

The *spino-occipital column* in Silurus is, like that of all other fishes, the direct continuation of the cervical gray matter, and it reaches rather far ventrally. Its frontal extremity extends less far forward than in several other teleosts.

Since this cell column exhibits the greatest frontal extension in those fishes where the tectum opticum is large and the ventral tecto-bulbar reflex paths are considerably developed, it may be that the smaller degree of this frontal extension in Silurus is a result of the small optic system of this animal.

A striking feature in the brain of this animal is the considerable development of the *lateralis system,* which I shall treat now together with the vestibular system.

Examining sections of the oblongata of Silurus in the caudo-frontal direction, one is struck by the great development of the crista cerebellaris which covers the massively developed dorso-lateral region of the bulb. At its most caudal level there is only one rather small crista, lying between the nervus lateralis posterior and the lobus sensibilis IX + X (fig. 10).

Some sections more frontally, where the posterior lateral nerve has penetrated into the bulb, another crista is added to this, remaining independent from it and located more laterally.

Proceeding in the frontal direction, we find that the crista of the nervus lateralis posterior (this is the one that is added) grows much larger than the crista of the lobus nervi lateralis anterioris (the one that reaches most caudally) and pushes it more and more medially (fig. 9). In the rostral levels of the bulb the lobus nervi lateralis posterioris is about three or four times larger (fig. 6) than the lobus nervi lateralis anterioris, which is not surprising on account of the enormous size of the body of Silurus and the great number of lateral line organs.

Proceeding still farther forward, we find that the lobus nervi lateralis posterioris first acquires a connection with the cerebellum

in the usual way by a fusion of its crista cerebellaris with the lamina molecularis cerebelli (fig. 6). The medial lobe (the one belonging to the anterior lateral nerve) continues still a certain distance rostrad beneath the cerebellum and its connection with the lateral lobe, then fuses with the contralateral medial lobe and finally fuses also with the cerebellum, its crista connecting with the lamina molecularis cerebelli (fig. 5). By the larger caliber of its parallel fibers and their different color the crista of the medial lobe can be still distinguished from the lobus nervi lateralis posterioris throughout many sections.

The most important alteration which occurs rostrad is the considerable increase of the granular layer of the lobi, chiefly of their lateral parts (eminentia granularis cerebelli, *Franz*) causing an increase of the dorso-lateral part of the bulb, which is specially striking in siluroids and continues dorsad and frontad into the corpus cerebelli, which, in contrast with most other teleosts, has grown out in the frontal instead of the caudal direction.

The nervi laterales themselves show the following course (cf. the scheme, fig. 11):

The *nervus lateralis posterior* is a strongly developed root of medium sized fibers. It enters the medulla in the typical way, shifting gradually inward and upward (fig. 10). It is soon covered with the crista, from which in more frontal sections it is again farther separated by the considerable development of the granular layer.

More rostrally the crista, and also the granular layer, and the fibers of the nervus lateralis posterior then form a flat layer (fig. 6) of white substance on the latero-dorsal border of the lobe, the ventral part of which then contains also fibers of the nervus lateralis anterior.

In more frontal levels the crista on these fibers disappears (fig. 5), the gray substance belonging to the posterior lateral nerve decreases, and the bundle on the lateral border—split up by several cerebellar systems—terminates in the adjacent gray matter laterally of the cerebellum. These relations are in harmony with those found by Tello in the carp, where also bulbar and cerebellar fibers could be distinguished. The descending

fibers of this nerve (also mentioned by that author in the carp and by Johnston in Acipenser) were more difficult to trace.[18] It is interesting that these descending fibers have a course similar to and are accompanied by vestibular fibers. This close relation between fibers of the lateralis and vestibularis nerves is also present in other systems of these roots, as will appear from the following pages.

From beneath the crista a large number of arcuate fibers arise (figs. 6, 8, 10), which after decussation under the fasciculus longitudinalis posterior proceed in a frontal direction, constituting the fasciculus longitudinalis lateralis, or lemniscus lateralis, which ends in the torus semicircularis or corpus posticum of the midbrain. Other fibers, both crossed and uncrossed, seem to run in a caudal direction, probably forming a part of the descending octavo- or latero-motor system.

The *nervus lateralis anterior* enters the brain, as mentioned above (p. 9), with the motor and sensory V and sensory VII roots (fig. 5). It is the largest part of this complex, lying laterally of the sensory VII root, and it consists of a small number of very coarse fibers, lying directly on the VII root, and a much greater number of finer fibers having a more dorso-lateral position. Dorsally of the place of entrance of the nervus lateralis anterior we find a region of gray substance which forms the frontal continuation of the gray matter of the lobus lateralis posterior and is laterally bordered by fibers of the latter, which only disappear on a level frontal to the entrance of the nervus lateralis anterior.

The most frontal bundles of the anterior lateral nerve that enter the bulb contain fine fibers only and proceed dorsally in the direction of the cerebellum [fig. 11 (1)], where they disappear. Their number is fairly large and the fibers, although their neurites are thin, are very well myelinated. They have also been described by Tello in the carp (*loc. cit.*, p. 11). As soon as this dorsal root has disappeared in the sections, the other, greater

[18] Compare Tello, El encefalo de los teleosteos. Trabajos del laboratorio de Madrid, tomo 7, 1909, fig. 4; and also Johnston, The brain of Acipenser. Zool. Jahrb., vol. 15, 1909, p. 24, who traced the descending fibers of this nerve to the beginning of the cervical cord.

part of the lateralis enters, dorsally consisting of fine fibers and ventrally of very coarse fibers.

The finer fibers proceed to the dorsal gray [fig. 11 (2)], which is covered by the medial crista cerebellaris and is known under the name, lobus nervi lateralis anterioris (see above). Under this crista cerebellaris a considerable layer of fibers of the same character is found, consisting of descending fibers of this nerve, which extend throughout a large extent of that lobe. Thus, while the posterior lateral nerve ascends beneath the lateral crista of the bulb, the anterior lateral nerve descends beneath the medial crista. More caudally, as the other components of the V + VII complex successively enter the brain, the lateralis sends a great quantity of fibers between the sensory VII and the gray substance in which a great number of fine lateralis axones end.

These fibers are not all of the same caliber. We may distinguish coarse fibers lying on the sensory VII and finer fibers dorsally of them. Among the latter also some coarser fibers occur. The former, the finer fibers, proceed in two fairly large bundles in a mesial and ventral direction, then turn and continue their course frontad [fig. 5, fig. 11 (3)]. They can be traced, running beneath the medial crista, to the level where the posterior lateralis nerve ends. They probably terminate here in the adjacent gray substance, but may also cross the raphé and end on the other side of the brain. Tello also has mentioned crossing fibers of this group.

Apart from these ascending fibers, there is a more dorsal group of fine fibers [fig. 11 (4)], which turn in a frontal direction at about the same level as those last mentioned and spread within the gray substance of the lobus lateralis anterior, proceeding about as far frontally as the first mentioned fibers.

At the same level on which these fibers take a frontal turn other fibers take a caudal course. They have the same color as the preceding fibers but are somewhat stronger. They descend in part as a well defined round bundle [fig. 11 (5)], in part as diffuse fibers [fig. 11 (6), figs. 6, 7] and take their course in the lobus nervi lateralis anterioris beneath the medial crista described above.

At more caudal levels the more strong circular bundle (fig. 6, *d.lat.ant.circ.*) acquires more and more a lateral position (fig. 7, *C.t.lat.ant.*), lying at last next to the nervus lateralis posterior, and disappearing in the gray substance of the tuberculum acusticum. The fibers end in the gray substance lying beneath the crista and its fiber layer, the so-called dorsal nucleus of the acusticum which contains a great quantity of medium sized cells.

The coarse fibers of the nervus lateralis anterior [fig. 11 (7) and (8)], lying dorsally of the sensory VII, are remarkable on account of their enormous caliber, though their number is much smaller than that of the smaller fibers.

As soon as the sensory VII has entered the brain, they gather ventro-laterally from it, surrounding the VII at its peripheral end (fig. 6, *c.f.lat.ant.*). Then, continuing their course more and more in the medial direction, they can be traced caudad in the ventral region of the bulb, where they can be seen still in the region of the frontal vestibular root, disappearing successively in the environs of the nucleus tangentialis sive ventralis. I have not been able to decide whether they end in this nucleus, though it seems very probable (fig. 7, *Lat.ant.c.f.*).

Apart from these fibers, coarse lateralis fibers occur which accompany fibers of the first vestibular root, running medially. Other components of the anterior lateral nerve join the bundles of the fibrae arcuatae internae running either dorsally or ventrally from the sensory VII, interrupted or not interrupted in the tangential nucleus [fig. 11 (7)].

The secondary ascending fibers of the nervus lateralis anterior form a strong richly myelinated bundle that can be easily distinguished from the surrounding fiber tracts (figs. 6, 8, 10). Its most caudal fibers appear in the most dorsal part of the lobus lateralis between the gray matter and the crista. They run in a medial direction and cross the raphé (fig. 8) beneath the fasciculus longitudinalis posterior. As already stated above, the lobus lateralis medialis has its own fibers of this system. Together they form the lateral lemniscus, or fasciculus longitudinalis lateralis, which ends in the torus semicircularis of the midbrain which is the primitive homologue of the corpus quadrigeminum

posticum, so that the secondary lateralis tract has a course and ending similar to the secondary ascending octavus bundle in mammals.

Descending fibers from the lobus nervi lateralis anterioris can also be traced. They are, however, not so easily recognizable as the ascending system.

It is interesting, in view of the probable relations of their functions,[19] that the endings of the vestibular nerve show so many resemblances with those of the lateralis nerves.

The *nervus vestibularis* is not very strongly developed in Silurus, probably in correlation with the sluggish life of the animal, and it enters the brain by two roots (fig. 11; *cf.* Juge, *loc. cit.*, p. 98).

The most frontal root (fig. 6) enters the brain rather far ventrally in the bulb, and then divides into ascending and descending fibers. We find fibers which run between the spinal V and the sensory VII; ascending in this area they turn mesad. They are of the same character as the lateralis fibers of this region and many of them cross the raphé (fig. 11, *a*), the rest of them running forward and ending in the lobus lateralis anterior (fig. 6, *VIII a.t.*).

Wallenberg[20] also has demonstrated with Marchi's degeneration that the vestibular nerve in teleosts possesses crossing fibers. Exactly where these fibers end I have not been able to see. Some of the coarser lateralis fibers accompany this system.

Other descending fibers, likewise running between the spinal V and the sensory VII roots, descend in a dorso-medial direction and end in the most ventral part of the gray substance of the lobus lineae lateralis anterioris [fig. 11 (9) and fig. 6, *VIII a.t.*].

Several vestibular fibers of the first root also run directly beneath the crista, forming descending systems [fig. 11 (10)]. An

[19] G. H. Parker, The function of the lateral line organs in fishes. Bul. of the Bureau of Fisheries for 1904, Washington, 1905, vol. 24, p. 185. The lateral line organs are stimulated by water vibrations of low frequency, 6 per second. The skin, the lateral organs and the ear (meaning the labyrinth in toto—B.v.d.S.) form a natural group of sense organs. The organ of touch may be said to be the first generation, from which the lateral line system has been derived, and this in turn has given rise to the ear.

[20] Beiträge zur Kenntnisse des Gehirnes der Teleostier und Selachier. Anat. Anz., Bd. 31, 1907, p. 374.

important nucleus in the vestibular apparatus is the nucleus ventralis (fig. 7, *N.v.*) of Kappers[21] and Wallenberg,[22] described by Cajal[23] and Tello[24] under the name of tangential nucleus.

This nucleus is an important motor reflex center for the vestibular root [see for fibers ending in it, fig. 11 (9 *c*) and for those originating from it, fig. 7]. It is, however, also traversed by fibers (fig. 7) which run more latero-mesad, apparently accompanied by fibers originating from the cells of the nucleus which also run in a dorso-medial direction, taking their caudal course beneath the fibrae arcuatae internae [fig. 11 (9 *b*)].

In addition to these fibers the first vestibular root forms also a descending system, the spinal vestibular fibers [fig. 11 (12)]. More caudally these fibers run along the ventro-lateral periphery of the bulb, between the secondary VII tract and the nervus lateralis posterior. They keep this position during their caudal course, successively joining the fibers of the posterior lateral nerve (fig. 10, *s.VIII*[1]).

Besides these spinal VIII fibers there are others which descend beneath the lobus lateralis anterior [fig. 11 (10)] and still others which descend first in the peripheral part of the bulb and then are pushed mesially by the descending system that constitutes the second (caudal) vestibular root [fig. 11 (11)]. These fibers first run beneath the lobus lateralis posterior, but finally take their course beneath the lobus lateralis anterior (the latter part of their course not being indicated on my scheme (fig. 11).

The second vestibular root consists chiefly of descending fibers [fig. 11 (13)] which run through and terminate in the lobus lineae lateralis. I have not been able to see any ascending fibers of this root. In the more caudal levels, consequently, three descending vestibular tracts are found under the lobus lineae lateralis anterioris, one lying medially coming from the anterior

[21] The structure of the teleostean and selachian brain. Jour. Comp. Neur., vol. 16, 1906.

[22] *Loc. cit.*, Anat. Anz., Bd. 31, 1907.

[23] Sur un noyau special du nerf vestibulaire des poissons et des oiseaux. Travaux du laboratoire de recherches biologiques, fasc. 1 and 2, 1908.

[24] *Loc. cit.*, Trabajos, tomo 7, 1909, pp. 14 and 9.

vestibular root [fig. 11 (11)], the second one lying more laterally coming from the posterior vestibular root [fig. 11 (13)], and the third one still more laterally coming from the first root [fig. 11 (12)]. The second one descends farther caudally than the first one and can be traced as far back in the gray substance of the lobus lineae lateralis anterioris as the crista which covers it.

MORMYRUS CASCHIVE

Whereas in Silurus glanis I dealt with an animal whose taste organs, especially those supplied by the VII nerve, were very highly developed, Mormyrus gives me the opportunity of describing an object in which the lateral nerves, notably the nervus lateralis posterior, are hypertrophied.

In studying this animal I have come to conclusions which are entirely different from those of Sanders[25] and Victor Franz.[26] These conclusions appeared to me to be in accord with the fundamental division made in the sensory regions of the bulb by the American school, especially by Strong,[27] Herrick[28] and Johnston.[29]

Mormyrus resembles Silurus in so far as its optic system is poorly developed, being even smaller than in the latter.

The *oculomotor nerve* enters the brain as usual in the cleft between the inferior lobes and the base of the midbrain (fig. 12). The nerve is so small that its central relations cannot be detected with accuracy. It seems to me that the root arises from a small medial nucleus dorsally of the ganglion interpedunculare and probably also from a nucleus that has a more dorso-lateral

[25] Sanders, Contributions to the anatomy of the central nervous system in vertebrate animals. The brain of the Mormyridae. Phil. Trans. Roy. Soc. London, no. 173, p. 927, 1883.

[26] Das Mormyridenhirn, Zool. Jahrb, Bd. 32, 1912, pp. 465–492.

[27] The cranial nerves of the Amphibia. Jour. Morph., vol. 10, 1895.

[28] C. J. Herrick. See especially The cranial and first spinal nerves of Menidia. Jour. Comp. Neur., vol. 9, 1909, p. 153. I do not agree, however, with this author in his conclusions regarding the valvula cerebelli published in his work on the gustatory paths (Jour. Comp. Neur., vol. 15, 1905), which are due in considerable part to a wrong interpretation of these bulbar centers given by Sanders (*loc. cit.*).

[29] Johnston. See especially, An attempt to define the primitive functional divisions of the central nervous system. Jour. Comp. Neur., vol. 12, 1902.

position. The exact connection with these nuclei cannot, however, be found.

The medial nucleus extends through only six sections (of 25 micra each) and contains exquisite motor cells. The dorso-lateral nucleus is a part of a cell column which extends from some sections in front of the root level until one section caudally from it. The most caudal part of this column is separated from the frontal part; the caudal part is probably the dorso-lateral III nucleus. Its cells have the character of motor cells and fibers from it can be traced in a central direction. The cells of the dorsal nucleus are larger than those of the ventral. Six of them may be found in one section on either side of the raphé (fig. 12).

The *trochlear root* leaves the brain between what Franz has called the Mormyro-cerebellum and the Ichthyo-cerebellum, i.e., between the valvula cerebelli and the corpus cerebelli. The extramedullary course of the root is interesting in that it first runs dorsad over the Ichthyo-cerebellum and then, 16 sections in front of its exit, decussates with the contra-lateral root. This decussation lies free in the cranial cavity, that is, outside any part of the brain wall or ependymal membrane.

After the decussation the root shifts ventrally and caudally along the cerebellum and leaves the periphery of the brain as soon as this is possible, that is, between the Mormyro-cerebellum and the oblongata (fig. 14).

This course, though strange, is not unique in principle. A similar relation has been described by Huet[30] in Gadus, where it was pointed out that this strange course is due to the valvula. Here also the great hypertrophy of the Mormyro-cerebellum must be considered as its cause. The very frontal place of entrance of this root (still more frontal than in Silurus) may also be explained perhaps by the frontal growth of the cerebellum.

The central course of the IV nerve cannot be traced on account of its small size and the intricate net-work of fibers in this region. Nevertheless in comparison with the III root and nucleus the

[30] Notes on the trochlear and oculomotor nuclei and the trochlear root in the lower vertebrates. Proc. kon. Akad. van Wetensch. Amsterdam, March 23. 1911, p. 897.

IV nerve is more advantageously arranged, since the motor cells that must be considered as the IV nucleus clearly send out a small bundle of myelinated fibers (fig. 13) that turn in a latero-dorsal direction around the ventricle in the manner characteristic of the IV root. The connection with the extra-medullary root can, however, not be stated. The nucleus in question is very small and extends through three sections of 25 micra (fig. 13).

The *motor V root*, after having entered the bulb, runs in a dorso-medial direction. The root is fairly strong, but its fibers are not as thick as in Silurus. Its nucleus lies between two parts of the fasciculus longitudinalis lateralis (fig. 14), as often occurs in teleosts.

Passing in a caudal direction, the nucleus increases in size and, while its dorsal limit remains about the same, the ventral cells reach farther downward in the direction of the tegmentum of the bulb (fig. 15). The nucleus as a whole acquires by no means so ventral a position as in Silurus.

The *sensory V root* (fig. 14) enters the brain at the same level as the motor root, at first lying laterally of it. Its fibers progressively pass over into the bulb and are very thick. The root is accompanied by a column of gray substance which is not especially enlarged at the proximal extremity of the root, so that a distinct frontal sensory nucleus does not exist.

Shortly after its entrance the descending V tract passes between the motor V nucleus (medially) and (laterally) another nucleus of large cells in which VIII fibers end and which will be discussed later on (fig. 15, *n.VIII l.*). Caudally the tract has a more dorsal position, lying between the coarse fibers of the VIII root dorsally and motor VII fibers ventrally (fig. 16). After this it acquires its most medial position (fig. 17) which it soon leaves again, being pushed laterad by the communis gray (fig. 19). The sensory IX enters the brain running over the spinal V tract (fig. 18), but the first X root passes beneath it (fig. 19). Then, approaching the spinal cord, it acquires a peripheral position and enters the substantia gelatinosa of Rolando.

As in Silurus, I have not been able to trace the mesencephalic root of the V nerve with certainty. I do not, however, doubt

its existence, since van Gehuchten[31] and Tello[32] have shown its presence in the trout and van Valkenburg[33] has demonstrated it in Lophius.

The addition of vagus fibers to the descending V tract—so obvious in Silurus—was not so conspicuous in my Mormyrus preparations, but I think that I have seen some of its fibers passing into the spinal V tract.

While the *visceral sensory VII* was extremely large in Silurus, it is rather small in Mormyrus, being even the smallest of the communis nerves. It is not connected at its entrance with the V, as in Silurus, but only with its own motor root and the nervus lateralis anterior. Its fine fibers enter the brain medially of the coarse fibers of the VIII (figs. 16, 17). It runs over the spinal V and there splits up into two bundles. Here it is joined by the sensory IX (fig. 18). Together they run backward intimately connected and end in the dorsal lobe of the communis gray, in which no special facialis lobe can be distinguished. It may be even that some fibers of the VII terminate farther backward than the IX (see figure 18, where *IX s.* ends, but some VII fibers go still farther backwards).

In opposition to Franz, I consequently believe that Mormyrus must not be regarded as a 'taste fish' with an extremely developed sensory VII, but rather as a fish in which the distribution of the sensory VII is very small in comparison with most other teleosts. The nerve described by Franz as nervus facialis is certainly the nervus lateralis posterior and this difference in interpretation appears to be fundamental, because it leads to an entirely different conception of the peculiar characters of the Mormyrus brain, since it appears that the enormous development of the valvula cerebelli in this animal does not depend on an increase of taste organs and their connections, as Herrick deduced from the misleading interpretations of Sanders and as was also defended

[31] van Gehuchten, De l'origine du pathétique et de la racine superieure du trijumeau. Bul. Acad. des Sciences de Belgique, vol. 29, 1895, p. 437, fig. 3.

[32] *Loc. cit.*, Trabajos, tomo. 7, 1909, p. 22.

[33] Van Valkenburg, Die mesencephalische Trigeminus Wurzel. Folia Neurobiologica, Bd. 5, no. 4, 1911, p. 377.

by Franz, but on its connections with the lateralis nerve by means of the torus semicircularis and the lateral longitudinal fascicle, as I will describe below.

The *motor fibers of the VII nerve* (fig. 16, *VII m.*) have a very peculiar course for teleosts, since they do not ascend to the floor of the fourth ventricle in a dorso-caudal direction, but in a dorso-frontal direction (fig. 15, *m.VII*), so that the frontal knee-bend of the VII does not lie behind the level of entrance of its root, as it does in all teleosts as yet examined, but in front of it.

A similar condition has been described by Kappers[34] in reptiles. In both cases the frontal position of the knee-bend is caused by the fibrae arcuatae internae of the lateral lemniscus. That the lateral lemniscus and the fibrae arcuatae internae by which it is formed are very large in Mormyrus and extend far frontally is due to the enormous development of the lobi lineae lateralis, of which it is the chief secondary tract.

The motor root of the VII passes beneath the spinal V tract (fig. 16) and runs to the ventricle over the fasciculus longitudinalis lateralis (fig. 15) in a dorso-frontal direction. The frontal knee appears 12 sections in front of the root entrance. Turning backward it first runs dorso-laterally, then laterally of the fasciculus longitudinalis posterior, separated from this tract by a typical blood vessel (fig. 16).

The horizontal part of the root can be traced to a point some sections in front of the caudal level of the motor VII nucleus. Some sections in front of this level its fibers begin to turn in a ventral direction (fig. 17), but they are lost between the masses of the dorsal arcuate fibers lying here, so that here as in Silurus the motor root fibers of the VII are interrupted by the dorsal commissure. Probably not all the fibers of the root end at this level; a part of them seem to run farther backward, joining the posterior visceral motor column, which consequently in its frontal end contains both IX and VII cells, as is also described for

[34] Kappers, The migrations of the bulbar V, VI and VII nucleus and the concomitating changes in the course of their root fibers. Verhand. kon. Akad. van Wetensch. Amsterdam, Deel 16, Sectie 2, p. 63 and map on p. 58.

other fishes by Herrick in Menidia[35] and by Kappers in several other teleosts.[36]

The cells of the motor VII nucleus are larger than those of the eye-muscle nuclei and smaller than the adjacent reticular cells (fig. 16). The nucleus lies in the upper third part of the bulb and is separated from the floor of the ventricle only by the fasciculus longitudinalis posterior and the dorsal arcuate fibers (figs. 16, 17).

In the caudal direction the number of cells in the median line diminishes, while some lateral cells are added. In the most caudal sections the cells acquire a somewhat larger size and take a somewhat less deep stain. Some of them have come to lie next to the fasciculus longitudinalis posterior. It is difficult to define the exact caudal limit of the VII nucleus. It is very obvious that the chief VII nucleus in Mormyrus has a much more dorsal and also a more frontal position than in Silurus. The more frontal position may be partly due to the strange development of the dorsal arcuate fibers behind it, together with the small size of the taste nucleus. The lack of ventral migration is certainly due to the absence or small size of the secondary gustatory tracts in comparison with Silurus.

The posterior part of the VII nucleus, connected with the IX + X nucleus, extends some distance in the ventral direction (see the diagram, fig. 21).

As could be predicted from the small size of the III and IV nerves, the *abducens nerves* are very small. Only few fibers could be found leaving the ventral region of the bulb, about at the level of figure 17, in a frontal direction. The nucleus could not be delimited with certainty.

The *sensory IX root* has been mentioned already when dealing with the sensory VII, and it has been stated that in its caudal course before entering its nucleus it fuses with the sensory VII root (fig. 18). The root leaves the frontal pole of the communis

[35] Jour. Comp. Neur., vol. 9, 1899.

[36] Weitere Mitteilungen über Neurobiotaxis. no. VIII. Ueber den motorischen Glossopharyngeus und Facialis bei niederen Vertebraten. Folia Neurobiologica, Bd. 8, 1914, p. 383.

gray next to the ventricle above the fibrae arcuatae internae. First running frontally, it then turns laterally over the spinal V tract, curves backward again and leaves the brain. Whether its gray substance is mixed with that of the VII, lies medial to it, or caudad, could not be stated with exactness. It seems probable that most of its fibers end in front of those of the VII.

The *motor IX root* is small and enters the brain medially of the sensory IX at the same level. Shifting in a frontal direction along the sensory V tract, it then turns in a medial direction to the chief nucleus of the motor VII. It is very difficult to say whether the root leaves the nucleus again or whether its fibers split up in it. It seems possible that a part of the motor cells of the IX nucleus are joined with those of the motor VII nucleus, and that the rest are joined with the dorsal VII–IX–X column. A careful examination of my sections seems to show that IX fibers pierce through the VII nucleus and the fibrae arcuatae dorsales and run backward (to the dorsal VII–IX–X cell column?).

The *sensory X roots* are fairly strong bundles (fig. 19). The four sensory roots which I found enter the brain separated by short distances from each other. It is a striking fact that the sensory rootlets, before running to the ventricle, remain for some distance along the ventro-lateral border. Then they pass beneath the spinal V tract (fig. 19) and run to their gray in a somewhat frontal direction. This frontal deviation of the sensory X roots is, however, so trifling that the whole transverse course can be studied in a few sections.

Since there is no question of an hypertrophy of the sensory IX and X roots, the condition of these roots also is not in favor of Sanders' interpretation that the vagal apparatus is execssively developed.

As I mentioned before, the addition of somatic sensory fibers of the vagus to the spinal V tract is not so obvious as in Silurus, but I did not find evidence to doubt their presence in Mormyrus, since some of the vagus roots run so closely along the spinal V tract that a transfer of their fibers into the spinal V is very well possible, if not even probable.

The *motor X roots* are very small (fig. 19). They originate from a continuous column, of which the frontal extremity (which probably contains also motor VII and IX cells) is shifted in a ventro-lateral direction, as is often found in teleosts, as in the Pleuronectidae and in Gadus (in the latter this part even forms a separate group).[37] The ventro-lateral migration of this part has apparently taken place at the expense of the cells which were originally dorsal and which have disappeared in that region or become very few.

The cells of this column (fig. 19) are not very large as contrasted with the reticular cells which are scattered along and below the fasciculus longitudinalis posterior.

The motor roots—both those from the ventral and from the larger dorsal part—leave the bulb together with the sensory roots. Proceeding caudally the dorsal nucleus becomes stronger and consists of cells which resemble very much those of the trochlear nucleus and have a fan-like arrangement.

On the left side of my sections (the one that is represented in my diagrams) the *spino-occipital roots* could not be traced on account of injuries to the ventral part of the bulb on that side. The right side, however, showed the first spino-occipital root as a fairly strong root. The frontal limit of the spino-occipital column can, however, not be stated with exactness on account of the presence of a great many reticular cells in that region of the bulb. This is the reason why the spino-occipital column has not been indicated in my diagram.

The *vestibulo-lateralis apparatus* in Mormyrus shows great deviation from the normal condition in teleosts, this being chiefly caused by the hypertrophy of the primary, secondary and tertiary centers of the lateralis nerves, the peculiar development of which has several times given rise to misinterpretations of the brain of the Mormyridae, as recently by Franz (*loc. cit.*).

Aside from this author there have been others who made a similar mistake. Thus Sanders has ascribed the peculiar develop-

[37] Kappers, Die phylogenetische Entwicklung der motorischen Wurzelkerne in Oblongata und Mittelhirn. Folia Neurobiologica, Bd. 6, Sommer-Ergänzungsheft, p. 29.

ment of the sensory centers of the lateralis nerves to a supposed hypertrophy of the sensory roots of the branchial nerves. He considered the dorsal enlargement of the bulb behind the cerebellum as a magnified tuberculum impar of cyprinoids on account of its fusion in the mid-line and its position directly behind the cerebellum. Since the tuberculum impar of cyprinoids is the end-station of the visceral VII root, Sanders supposed that also in Mormyrus this taste nerve was exceedingly developed (*loc. cit.*, p. 951).

C. J. Herrick, who had no material of Mormyrus himself, in his work on the central gustatory paths[38] deduces from Sanders' description that the enormous development of the lateral lobes of the valvula cerebelli in Mormyrus is due to the exaggeration of gustatory functions. "It appears probable," he says, "that the lateral lobes are related to gustatory reflexes," although "the chief connections of the cerebellum are tactile, acusticolateral and visual." My own researches, which demonstrate that the visceral sensory nerves in Mormyrus are rather less than more developed than in an average form of teleost, and certainly much less than in cyprinoids, show that the interpretation of Sanders, as well as the conclusion drawn by C. J. Herrick, are mistaken, and that Franz's nomenclature of the nerves and consequently also his interpretation of the bulb are wrong.

Before dealing with the lateralis and vestibular nerves I shall briefly describe the general morphology of the centers in question, from which it will appear that their general relations (though they are enormously increased in size) can be compared with the conditions of the same systems as found in Silurus.

In Silurus we could distinguish the lobe of the nervus lateralis posterior by its lateral position from the lobe of the anterior lateral nerve, which occupies a more medial position and extends farther backward. Both lobes, the lateral and the medial, increase in size in more frontal sections and fuse in the dorsal midline with the contralateral lobes. The lobe of the posterior lateral nerve, that is the more lateral lobe, increases in size

[38] *Loc. cit.*, Jour. Comp. Neur., vol. 15, 1905, p. 452.

farther forward, however, much more than the medial lobe, and at the place where both lobes have fused with their contralateral structures the fusion of the lateral lobes lies dorsally of the fusion of the medial, forming the larger arch of the two. Both then continue into the cerebellum by a fusion of the crista cerebellaris with the molecular layer of the cerebellum.

The relations as found in Mormyrus bear a great resemblance to those in Silurus in that here also the lobe of the posterior lateral nerve is by far the larger of the two. Since, however, both are hypertrophied in Mormyrus, the fusion of each with its contralateral formation—which fusion in Silurus occurs only in the more frontal sections—is present in Mormyrus over the whole extent of the lobes. And since the medial lobe (related to the anterior nerve) is entirely covered by the enormously increased lateral lobe, the entire center makes the impression of consisting of one tuberculum impar (cf. figure 6 of Silurus with figure 19 of Mormyrus).

The only differences between the two animals, consequently, are matters of degree, being: first, that in Mormyrus the dorsal fusion of the homologus lobes takes place over the whole extent of the formation; second, that the greater size of the lateral lobe (of the posterior nerve) as compared with the medial lobe (of the anterior nerve) is so much increased that it is not the medial lobe which extends farther caudad but the lateral one, and this overlies the former not only dorsally but also caudally; and third, the contribution of the nervus lateralis anterior to the lobe of the nervus lateralis posterior of Mormyrus is much larger than that of Silurus.

It will appear in the following description that the secondary tract from these lobes, the fasciculus longitudinalis lateralis, is correspondingly increased and that the midbrain nucleus of that tract, the torus semicircularis, is in turn connected with the valvula cerebelli, especially with its lateral lobes, the enlargement of which thus depends on the lateralis systems and their secondary connections and not on the poorly developed taste nerves.

The entrance and courses of the lateral nerves are as follows:

The *nervus lateralis anterior*, vestibularis and facialis form one complex (figs. 15, 16, 17), of which the lateralis anterior is the largest component and enters the bulb farthest frontally (fig. 20). Its fibers run as a very large bundle in a dorso-medial direction to end in the dorsal unpaired gray substance that is covered by the crista cerebellaris [fig. 15, fig. 20 (1)].

The root passes between a coarse fibered tract, lying laterally, the tractus spino-cerebellaris, and a region of gray matter which separates it from the spinal V tract (fig. 15, *n.VIII l.*). This gray matter contains the nucleus mentioned above (see p. 28) which consists of rather large cells. The frontal pole of this nucleus lies more dorsally than its caudal pole and frontally the nucleus is continuous with the gray substance of the nervus lateralis and medially with that of the vestibularis (fig. 15, *n.VIII*). Whether this nucleus is the homologue of the nucleus ventralis VIII in other fishes (nucleus tangentialis of Cajal and Tello) cannot be stated with certainty, but this is most probable.

Not all the fibers of the nervus lateralis anterior end in the unpaired dorsal gray. It appears that a considerable part [fig. 20 (2)] of the fibers run backward forming a descending tract, just as in Silurus. Whether this tract is formed by bifurcation of the entering root fibers I cannot say, but it seems quite possible. The descending tract continues caudad for several sections in the same region of the bulb in which it first appears, then it shifts more laterally and proceeds in a dorsal direction laterally from the spino-cerebellar tract (fig. 16). It then forms a part of the substance which Franz[39] has called lobus facialis, but which really is the lobus lineae lateralis. It is provided with granular cells and covered by a crista cerebellaris which is separated from its white substance by a double row of large cells.

The nervus lateralis anterior is the most lateral component in the complex of root fibers at the level of entrance. The distinction between it and the nervus vestibularis is not, however, always easy to make. Then, some sections more caudad, after

[39] Zool. Jahrb., Bd. 32, Tafel 26, fig. 6.

the lateralis fibers have reached the dorsal unpaired nucleus, another set of fibers runs dorsally and laterally to the gray substance above mentioned. It may be that these are vestibular fibers, though I do not consider it very probable. As a rule there is considerable difference between lateralis and vestibularis fibers, the former being more fine and compact, the latter in part coarser and in part a great deal finer.

The *nervus lateralis posterior* is very large in Mormyrus. I cannot understand how Sanders (*loc. cit.*, p. 53) was not impressed by its considerable size.

While in Silurus the whole of it enters on the level of the glossopharyngeus (fig. 10), its entrance in Mormyrus extends as far backward as the second vagal root, as a result of the considerable backward enlargement of its corresponding lobe. Within the bulb the nerve runs some sections frontad and then sends a strong bundle of nerve fibers [fig. 19 and fig. 20 (3)] into the dorsal lobus lineae lateralis posterioris, occupying the same position as fibers of the nervus lateralis anterior, but caudally from them. These fibers also are covered by the double row of large cells of the crista (fig. 19).

The relations as found in Mormyrus are very much in favor of Johnston's[40] conception concerning the relation between the lobus lineae lateralis and the cerebellum, which here resemble each other still more than in Silurus, for, in addition to the great resemblance between the molecular layer and the crista cerebellaris, the relation between the Purkinje cells of the cerebellum and the large cells of the crista cerebellaris is more striking than in Silurus.

I will again emphasize here that the fibers which Franz has described as facial fibers (*loc. cit.*, Tafel 26, fig. 6) are fibers of the nervus lateralis posterior.

Not all the fibers of the nervus lateralis posterior pass directly into the dorsal lobe. Some of them—be it by bifurcation or as separate tracts—run directly forward [fig. 20 (4)] after their entrance into the bulb. Piercing the coarse-fibered tract of the spino-cerebellar bundle (fig. 18), they end in the more ventral

[40] The brain of Petromyzon. Jour. Comp. Neur., vol. 12, 1902, p. 1.

part of the gray matter (covered with crista) in which also fibers of the anterior lateral nerve terminate (figs. 16, 17).

Laterally of the entrance of the lateralis posterior a group of cells is found (fig. 19) which extends (with slight interruptions) to the place of entrance of the nervus lateralis anterior. Caudad it is still found in several sections behind the lateralis posterior. The processes of these cells are directed in a medial direction. One might call this group the nucleus lineae lateralis (figs. 17, 16, 15). The secondary fibers arising from the lateralis lobes are very numerous (fig. 15) and form a very big decussation in the dorsal part of the raphé, the same as in other teleosts but much larger (figs. 16, 17).

Many of these fibers of the lobus lineae lateralis posterioris pierce through the underlying crista of the lobus lateralis anterior (fig. 17). The majority of these fibers ascend, after the decussation, in two separate bundles (fig. 15), which join farther frontally (figs. 12, 13). Most of them, if not all, reach the torus semicircularis, which again is connected with the valvula of the cerebellum, especially with its lateral lobes, by the tractus cerebello-mesencephalicus dorsalis.

It is not my intention to deal with further details of the secondary connections of the lateralis centers, but I mention this only to show that the considerable development of the valvula cerebelli in this animal does not depend on 'taste,' but on the great size of the lateralis nerves and their secondary and tertiary connections.

In dealing with the *vestibular nerve*, I shall describe separately the course of its coarse and fine fibers.

The coarse fibers[41] of the VIII nerve enter the brain behind the nervus lateralis anterior. They constitute the most medial and most frontal part of the vestibular root and take a dorsofrontal course [fig. 20 (5)]. As a strong coarse-fibered bundle they pass along the lateral and dorsal border of the spinal V tract (fig. 16) and end in the region of gray substance[42] that lies

[41] Outside the medulla oblongata they join the fibers of the nervus lateralis anterior.

[42] This region lies beneath the fibrae arcuatae internae.

medially and ventrally from the end-nucleus of the nervus lateralis anterior (fig. 15). In this region large faintly colored cells are found everywhere.

The finer fibers of the vestibular nerve form the most lateral and caudal part of that nerve [fig. 20 (6)]. Part of them pass in a frontal direction after their entrance into the bulb, and shifting laterally along the coarse fibers (fig. 16) mentioned above they partly go to the medial unpaired nucleus of the nervus lateralis anterior (fig. 15), partly end in the ventro-lateral gray substance, in which also fibers of the posterior lateral nerve terminate (fig. 14).

Apart from these frontal root fibers, a set of fibers [fig. 20 (7)] enters the bulb directly behind the frontal ones (not separated from them), which also first take a fronto-dorso-medial course but then seem to bifurcate so that an ascending part of them runs to the region of the lobus lateralis anterior, while the descending fibers (figs. 16, 17, *b.f.VIII*) run backward in a horizontal direction and then, passing through the fibrae arcuatae dorsales, also split up in the gray substance of the lobus lateralis anterior (fig. 18) caudally from the entrance of the root. I have been able to distinguish with great accuracy the two bundles here mentioned, and need not say that also at the level of entrance itself vestibular fibers end in the gray matter of the nervus lateralis anterior (fig. 17).

CONCLUSIONS

After this exposé of the cranial nerves of Silurus and Mormyrus, I will briefly discuss the results. Comparing the diagram of the motor nuclei and roots of Silurus with those of Tinca (fig. 21), we see that in both the motor V and motor VII nuclei have acquired a very ventral position. Both fishes are pronounced 'taste fishes' and it is probable that this ventral position of the V and VII nuclei in both is due to the same cause.

This cause is the considerable development of the anterior secondary gustatory tract and the shorter reflex gustatory paths that may accompany it. The anterior secondary gustatory tract

having a very ventral position along the spinal V tract, with which it may be correlated, it is not surprising to find the motor cells in question lying along it.

There is, however, a difference between Tinca and Silurus regarding their VII cells, in that, while in Tinca some of these cells still remain in the dorsal IX + X column, in Silurus all of them appear to have descended to form the fronto-ventral nucleus.

The motor V nuclei in both fishes also are strikingly similar, not only by reason of their position, but also by reason of the fact that in both animals a division, or at least an obvious indication of a division, into two groups of cells is visible.

We do not know what this division means. It seems probable that it is caused by the caudal shifting of the posterior cells of the nucleus, which may be more under the influence of the stimulation of the gustatory fibers that reach the nucleus from behind. This separation is also indicated in the root during its intrameduallary course in Silurus, as seen in figure 4.

The IX and X cells retain their dorsal position in the motor column of the vagus.

The reduction of the eye-muscle nuclei in Silurus is interesting. The reduction of the visual apparatus and hypertrophy of taste in bottom feeders has also been emphasized by Herrick. The trochlearis root leaves the brain in a very frontal position, in this respect being only surpassed by Mormyrus. It is probable that the frontal entrance of the IV root in Silurus and Mormyrus are both due to the considerable development of the valvula.

Mormyrus, which is no 'taste fish' at all (as an accurate examination of its root fibers shows), exhibits entirely different relations of the V and VII nuclei. Both nuclei have kept a more dorsal position and they do not lie in the same region of the brain, so that there is nothing in favor of their place being defined by the same system as in the other fishes mentioned. The V nucleus extends a little ventro-laterally in the direction of the reticular substance of its own sensory root, and the VII nucleus remains far dorsally. The latter has also a more frontal position. The less caudal, but especially the less ventral position, of the motor

VII nucleus is due to the small development of the secondary taste system.

The ventro-lateral migration of the frontal cells of the IX column (containing probably VII and IX cells) is more pronounced than in most other teleosts.

Regarding the sensory roots, I may emphasize the fact that Silurus glanis, like the North American siluroid fishes examined by C. J. Herrick, exhibits a considerable hypertrophy of the sensory branchial system, especially of the sensory VII, which by means of the ramus recurrens facialis innervates the taste buds of the body. In contrast with cyprinoids, the sensory system of the IX and X nerves is not so much hypertrophied. According to Herrick this is chiefly due to the absence of the palatal organ, which in cyprinoids contains an enormous number of vagal taste buds.

In Mormyrus, contrary to the statements made by Sanders and Franz, the sensory system of the branchial nerves is very poorly developed; but the lateralis nerves, especially the posterior ones, attain a size which is much more conspicuous than in siluroids.

The development of the lateralis system has given rise to the formation of what Sanders has called the tuberculum impar faciale and the vagal lobes (*loc. cit.*, p. 51), but which really are the lateralis lobes of both sides fused in the dorsal mid-line. The conclusion which Herrick (who had no material of Mormyrus at his disposal) has drawn from the erroneous statements published by Sanders (viz., that the hypertrophy of the lateral lobes of the valvula cerebelli in Mormyrus are due to their relations with the centers of taste) consequently has to be discarded.[43]

It seems to me that Herrick's own researches already made this supposition improbable. The sharp delimitation of the visceral and somatic sensory centers, so often demonstrated by Herrick himself, holds also good for the brain of Mormyrus, in

[43] The argument used by this author, that the fishes here under consideration, unlike most other vertebrates, make somatic movements in response to cutaneous gustatory stimulation, does not seem convincing to me, and moreover has not been proved for Mormyrus.

which the hypertrophy of the lateral lobes of the valvula cerebelli is due to the special development of secondary connections of the lateralis nerves, the primary centers of which also show so intimate a relation with the cerebellum.

It is a great pleasure to me to refer here also to the paper published by Stendell,[44] which appeared after I had completed the results of my researches, and which agrees in most respects with my own results. Stendell's work is a valuable addition to our knowledge of Mormyrus.

POSTSCRIPT

After this paper had already been sent to the printers another contribution by Stendell appeared in the Verhandlungen der Deutschen zoologischen Gesellschaft auf den 24. Jahres-versammlung zu Freiburg in Br., 1914, entitled, Morphologische Studien an Mormyriden.

In this article he states that, looking for an explanation for the excessive developement of the nervi laterales in Mormyrus, he found peculiar gland-like organs in the lips of this animal, innervated by the nervus lateralis anterior. Stendell was inclined to admit a correlation between the considerable development of the Mormyro-cerebellum and these organs, concerning the function of which he was not able to pronounce an opinion but which—on account of their innervation—he regarded as belonging to the group of acoustico-lateral organs. Since he says he has found a branch of the anterior lateral nerve innervating taste buds of the tongue, it is a great pity that he does not say whether these fibers, which peripherally run with the nervus lateralis anterior, do or do not separate from the other fibers of this nerve after their entrance into the central nervous system.

The cruel war which demands so many victims in Europe has also killed this young neurologist, whose work on Mormyrus led us to expect a great deal from him in the future. Science knows of no nationalism, and we all regret his sudden death.

[44] Abhandlungen der Senkenbergischen naturforschenden Gesellschaft, 1914.

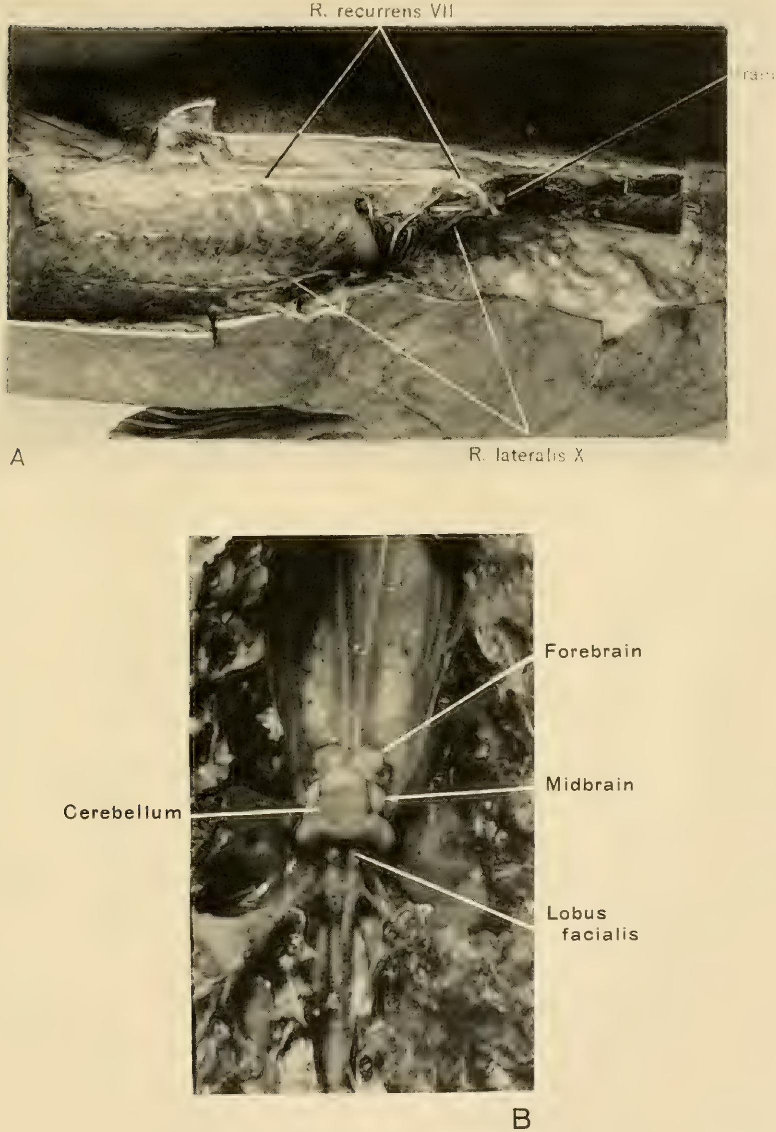
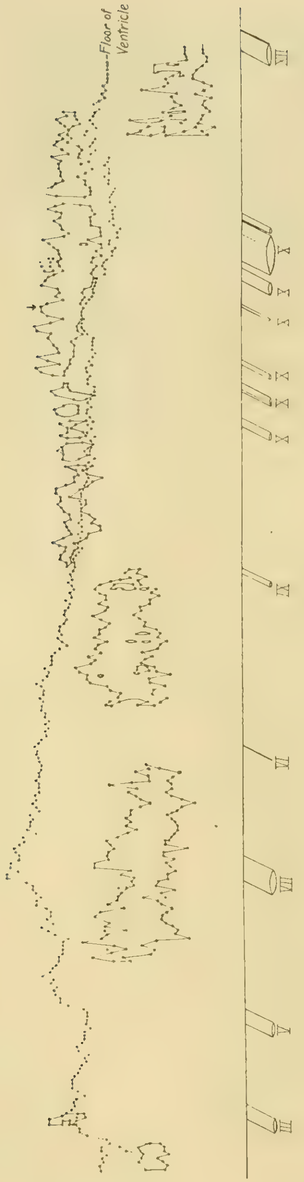


Fig. 1 Two dissections of the head of Silurus glanis, to illustrate the relations of the brain and nerves (made by Mr. Schepman); *A*, from the side; *B*, from above.



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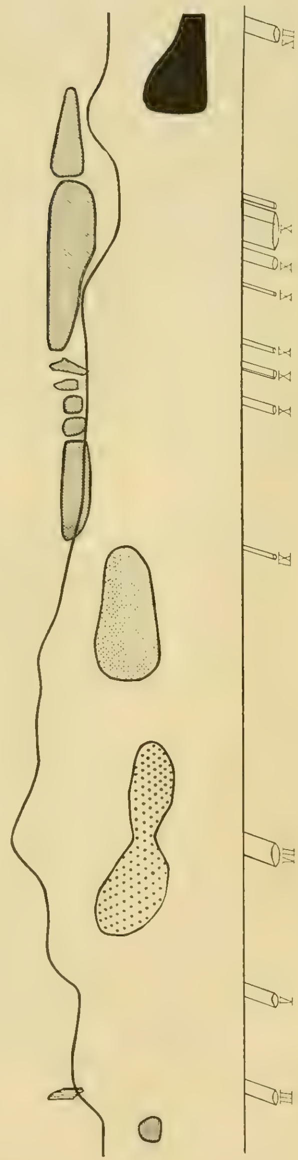

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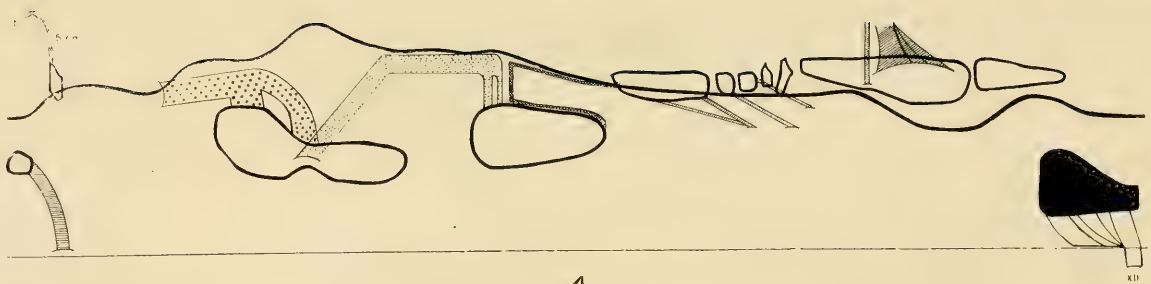

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Fig. 2 A projection on the sagittal plane of the motor nuclei of the medulla oblongata of Silurus glanis. × 10. The ventral surface is drawn as a straight line (which involves only a slight error); the dorsal surface, in the median raphé, is drawn as a broken line; and the outlines of the motor nuclei are drawn in continuous lines.

Fig. 3 A projection of the motor nuclei and roots of the medulla oblongata of Silurus glanis, based on figure 2 and conventionalized to accord with Kappers' diagrams.

Fig. 4 A projection similar to that of figure 3, to illustrate the exact superficial origins and central courses of the motor roots in Silurus glanis.

Figs. 5 to 10 A series of cross sections through the medulla oblongata of Silurus glanis at the levels indicated in figure 11.

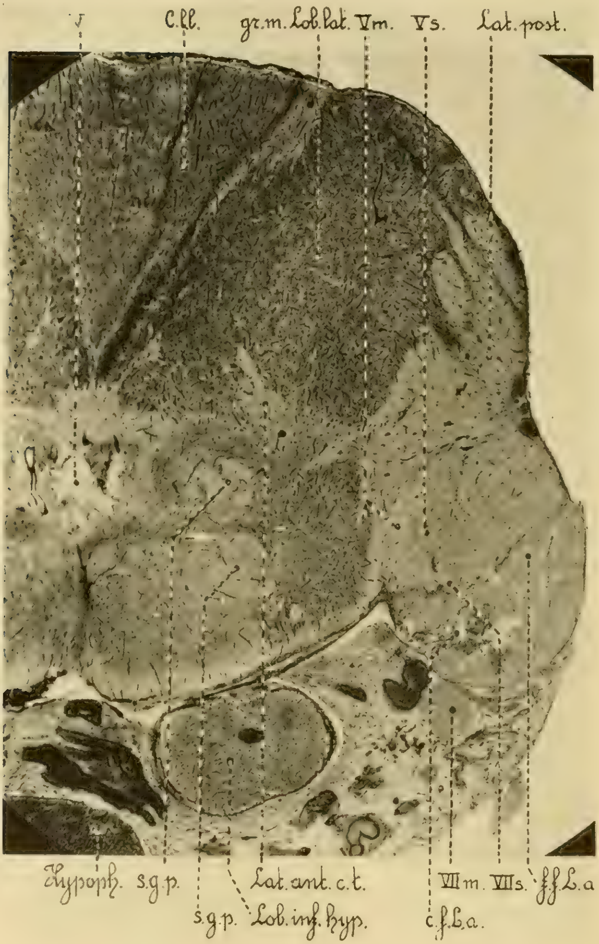


Fig. 5 Section at the level of the V roots. *c.f.L.a.*, coarse fibers of nervus lateralis anterior; *C.l.l.*, crista lobi lateralis; *f.f.L.a.*, fine fibers of nervus lateralis anterior; *gr.m.lob.lat.*, gray matter of lobus lateralis; *Hypoph.*, hypophysis; *Lat.ant.c.t.*, cerebellar tract of nervus lateralis anterior [fig. 11 (1)]; *Lat.post.*, nervus lateralis posterior; *Lob.inf.hyp.*, lobus inferior hypothalami; *s.g.p.*, secondary gustatory path (Herrick) going to the Rindenknoten mesencephali (Mayser); *V.*, ventricle; *V m.*, motor root of trigeminus; *V s.*, sensory root of trigeminus; *VII m.*, motor root of facialis; *VII s.*, sensory root of facialis.

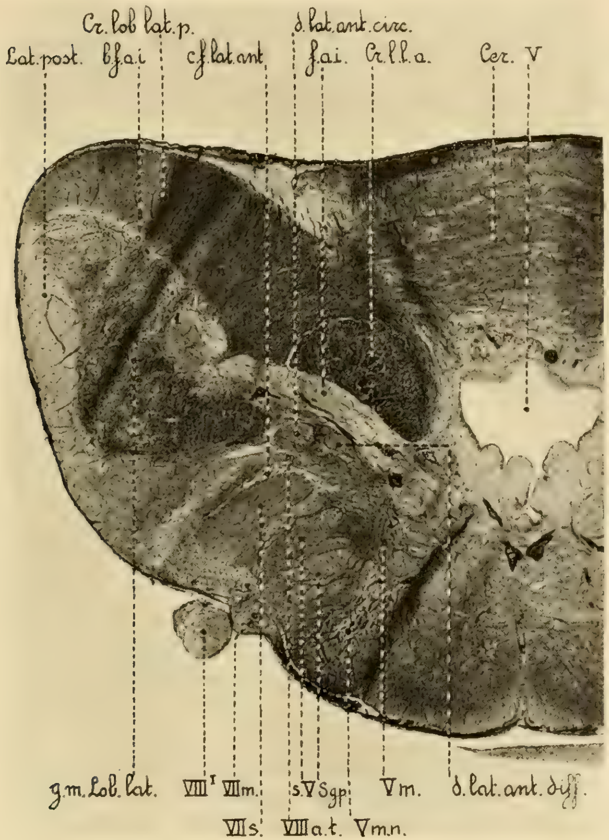


Fig. 6 Section shortly in front of the VIII roots. *b.f.a.i.*, beginning of the fibrae arcuatae internae; *Cer.*, cerebellum; *c.f.lat.ant.*, coarse fibers of nervus lateralis anterior; *Cr.l.l.a.*, crista lobi lineae lateralis anterioris; *Cr.lob.lat.p.*, crista lobi lineae lateralis posterioris; *d.lat.ant.circ.*, circular descending tract of nervus lateralis anterior ending beneath the lobus lateralis posterior [fig. 11 (5)]; *d.lat.ant.diff.*, diffuse descending tract of nervus lateralis anterior (fine fibers) ending under the lobus lateralis anterior [fig. 11 (6)]; *f.a.i.*, fibrae arcuatae internae; *g.m.Lob.lat.*, gray matter of lobus lateralis posterior; *Lat.post.*, nervus lateralis posterior; *S.g.p.*, secondary gustatory path; *s.V.*, spinal V tract; *V.*, ventricle; *V m.*, motor root of trigeminus; *V m.n.*, motor V nucleus some sections behind its isthmus; *VII m.*, motor VII root just entering the bulb; *VII s.*, sensory VII root; *VIII¹.*, first root of VIII nerve; *VIII a.t.*, ascending tract of first VIII root [fig. 11 (9)], after having given off the branches indicated in figure 11, *a*, *b*, and *c*, now turning forward under the lobus lateralis anterior.

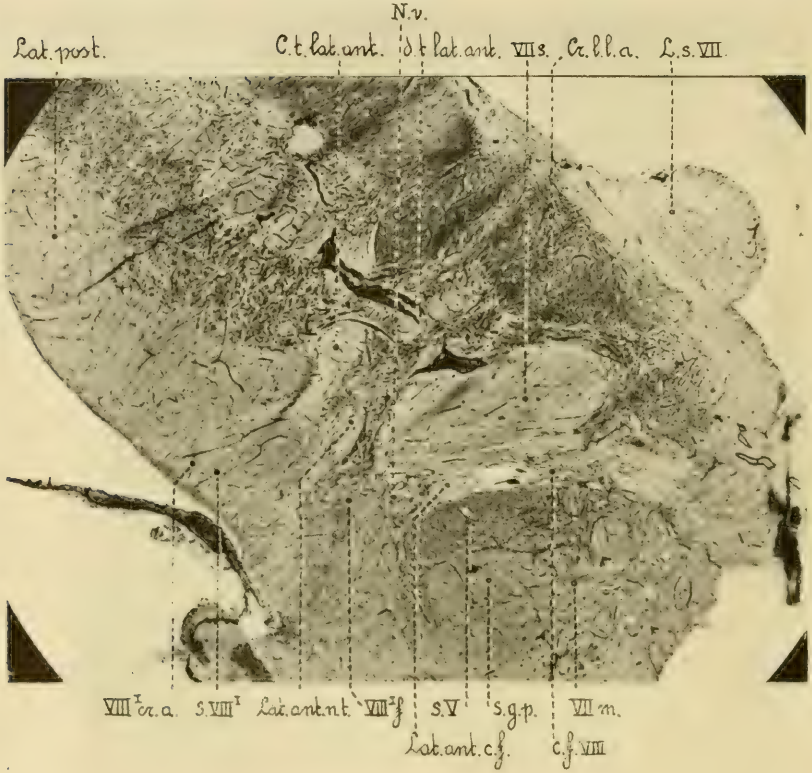


Fig. 7 Section at the level of the first VIII root. *c.f.VIII*, coarse fibers of the VIII root traversing the nucleus ventralis, with some coarse fibers of the nervus lateralis anterior and fibers originating from the nucleus tangentialis of Cajal [fig. 11 (9 *b*)]; *Cr.l.l.a.*, crista lobi lineae lateralis anterioris; *C.t.lat. ant.*, circular descending tract (fine fibers) of nervus lateralis anterior [fig. 11 (5)]; *d.t.lat.ant.*, diffuse descending tract of nervus lateralis anterior [fig. 11 (6)]; *Lat. ant.c.f.*, coarse fibers of nervus lateralis anterior [fig. 11 (7)]; *Lat. ant.n.t.*, coarse fibers of nervus lateralis anterior, probably ending in the nucleus tangentialis of Cajal [fig. 11 (8)]; *Lat.post.*, nervus lateralis posterior; *L.s.VII*, lobus sensitivus VII (lobus facialis); *N.v.*, Nucleus ventralis (Kappers) sive tangentialis (Cajal); *s.g.p.*, secondary gustatory path; *s.V.*, spinal V tract; *s.VIII*[1], spinal tract of first VIII root [fig. 11 (12)]; *VII m.*, motor VII root; *VII s.*, sensory VII root; *VIII*[1] *cr.a.*, descending tract of first VIII root ending beneath the lobus lateralis anterior [fig. 11 (11)]; *VIII*[1]*f.*, fine fibers of the first VIII root [fig. 11 (9)], going forward and sending out the three varieties of fibers, 9, *a*, *b* and c.

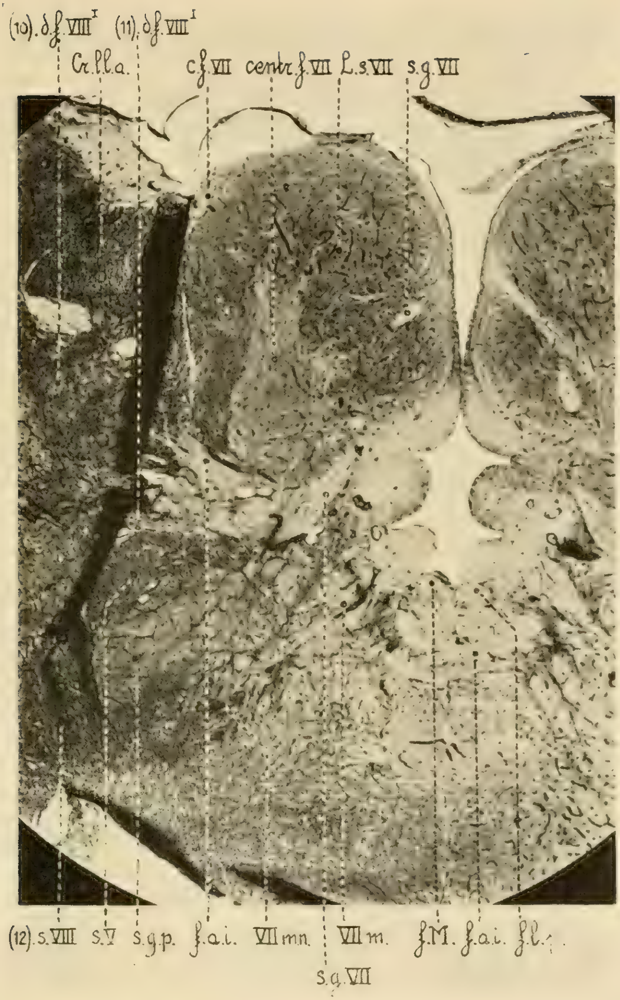


Fig. 8 Section at the level of the second VIII root. *centr.f.VII*, central fibers of the sensory VII; *c.f.VII*, some capsular fibers of the sensory VII; *Cr.l.l.a.*, crista lobi lateralis anterioris; *f.a.i.*, fibrae arcuatae internae crossing the raphé; *f.l.p.*, fasciculus longitudinalis posterior; *f.M.*, Mauthner's fiber; *L.s.VII*, lobus sensitivus VII; *s.g.p.*, secondary gustatory path directed toward the mesencephalon; *s.g.VII*, secondary VII (gustatory) fibers; *s.V*, spinal V tract; *VII m.*, descending part of motor VII root; *VII m.n.*, motor VII nucleus; *(10) d.f.VIII[1]*, descending tract of first VIII root, going direct to the lobus lateralis anterior [fig. 11 (10)]; *(11) d.f.VIII[1]*, descending tract of first VIII root, ending beneath the lobus lateralis anterior [fig. 11 (11)]; *(12) s.VIII*, spinal VIII tract [see fig. 11 (12)].

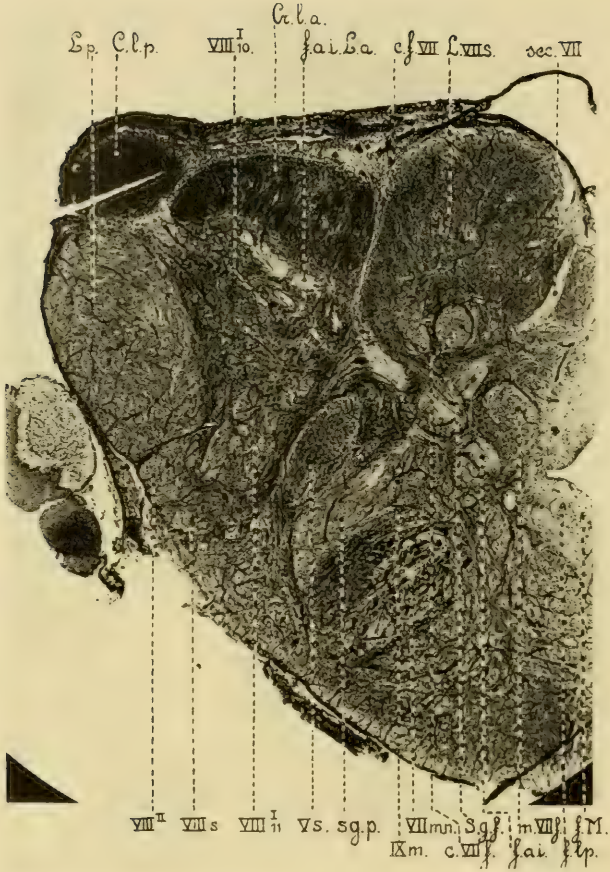


Fig. 9 Section between the second VIII root and the IX roots. *c.f.VII*, capsular fibers of the sensory VII; *C.l.p.*, crista lobi lateralis posterioris; *Cr.l.a.*, crista lobi lateralis anterioris; *c.VII f.*, central fibers of the sensory VII root descending as a circular tract for several sections; *f.a.i.*, fibrae arcuatae internae; *f.a.i.L.a.*, fibrae arcuatae internae originating from the lobus lateralis anterior; *f.l.p.*, fasciculus longitudinalis posterior; *f.M.*, Mauthner's fiber; *IX m.*, motor IX root piercing the secondary gustatory tract; *L.p.*, nervus lateralis posterior; *L.VII s.*, lobus sensiblis VII; *m.VII f.*, fibers from the sensory VII root which pass mesially and then descend as a circular tract; *sec.VII*, secondary (gustatory?) fibers originating from lobus VII; *s.g.f.*, secondary gustatory fibers crossing the fibrae arcuatae internae; *s.g.p.*, secondary gustatory path; *V s.*, spinal V tract; *VII m.n.*, motor VII nucleus; $VIII^{11}$, second VIII root [fig. 11 (13)]; $VIII^{1}$ *10*, fibers of the first VIII root, descending beneath the lobus lateralis anterior [fig. 11 (10)]; $VIII^{1}$ *11*, fibers of the first VIII root, descending medially of those of the second VIII root [fig. 11 (11)]; *VIII s.*, spinal VIII tract from first VIII root [fig. 11 (12)].

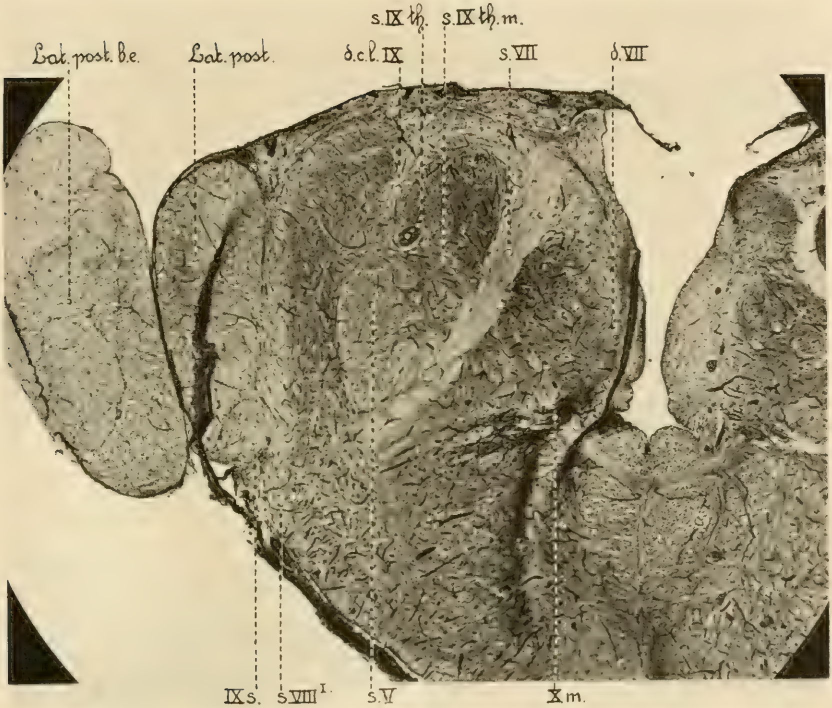


Fig. 10 Section at the level of the glossopharyngeal and upper vagus roots. *d.c.l.IX*, fibers for the dorso-lateral capsule of the lobus glossopharyngei; *d.VII*, descending VII root, medial fibers (fig. 9, *m. VII f.*); *IX s.*, sensory IX root at its entrance; *Lat.post.*, nervus lateralis posterior; *Lat.post.b.e.*, nervus lateralis posterior before its entrance into the bulb., *s.IX th.*, thinner fibers of the sensory IX root; *s.IX th. m.*, thicker fibers of the sensory IX root directed mesad; *s. V*, spinal V tract; *s. VII*, secondary VII fibers (probably for the greater part gustatory); *s. VIII*[1], descending fibers of first VIII root [fig. 11 (12)]; *X m.*, motor root of vagus.

Fig. 11 Diagram of the relations of the VIII and lateralis roots of Silurus glanis; compare figures 5 to 10.

Nervus lateralis anterior:

(1) cerebellar tracts.

(2) fine fibers going to the lobus lateralis anterior.

(3) two bundles of fine ventrally ascending fibers.

(4) diffuse fine dorsally ascending fibers.

(5) circular bundle of fine descending fibers ending beneath the lobus lineae lateralis posterioris.

(6) diffuse bundle of fine descending fibers ending beneath the lobus lineae lateralis anterioris.

(7) coarse fibers probably ending in the substantia reticularis ventralis or crossing with fibrae arcuatae internae.

(8) coarse fibers probably ending in nucleus ventralis VIII (Kappers).

Octavus:

(9) ascending bundle of fibers that probably gives off (a) fibers crossing the raphé; (b) fibers piercing the nucleus ventralis VIII (perhaps crossing the raphé); (c) fibers ending in the nucleus ventralis.

(10) tract descending directly beneath the crista lobi lineae lateralis anterioris, not piercing the nucleus ventralis VIII.

(11) tract, farther on, descending beneath the crista lobi lineae lateralis anterioris medially from the secondary VIII root.

(12) spinal VIII tract.

(13) second VIII root.

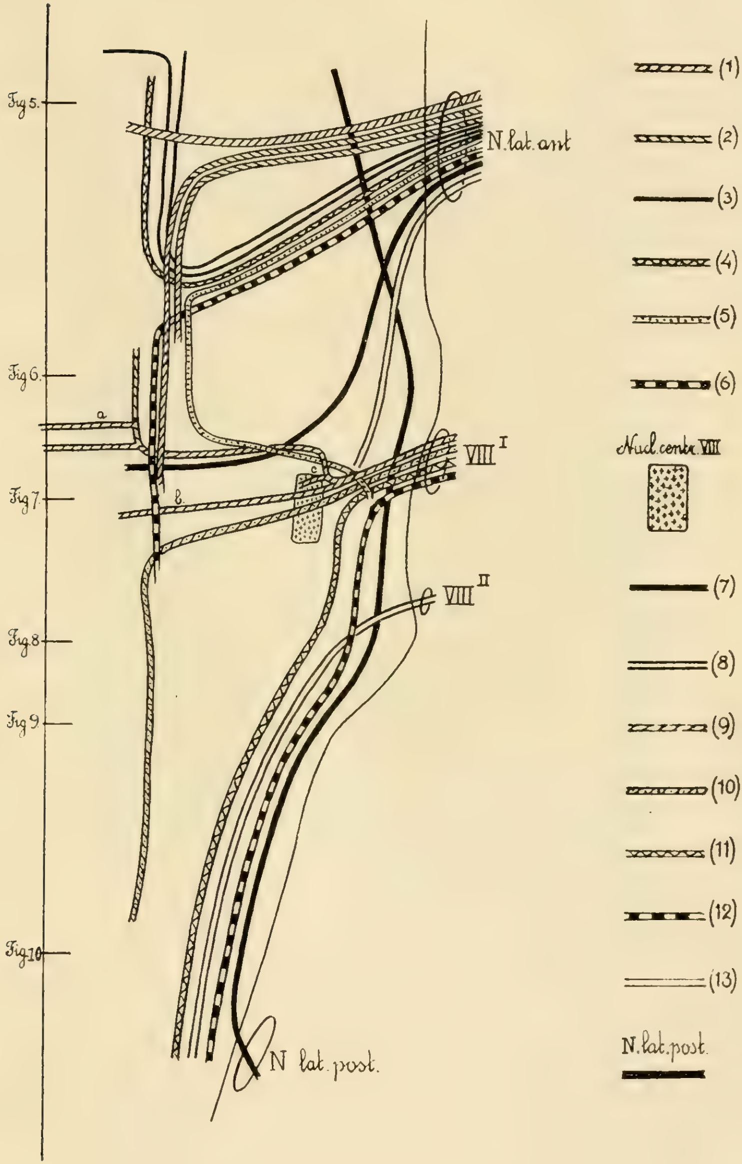
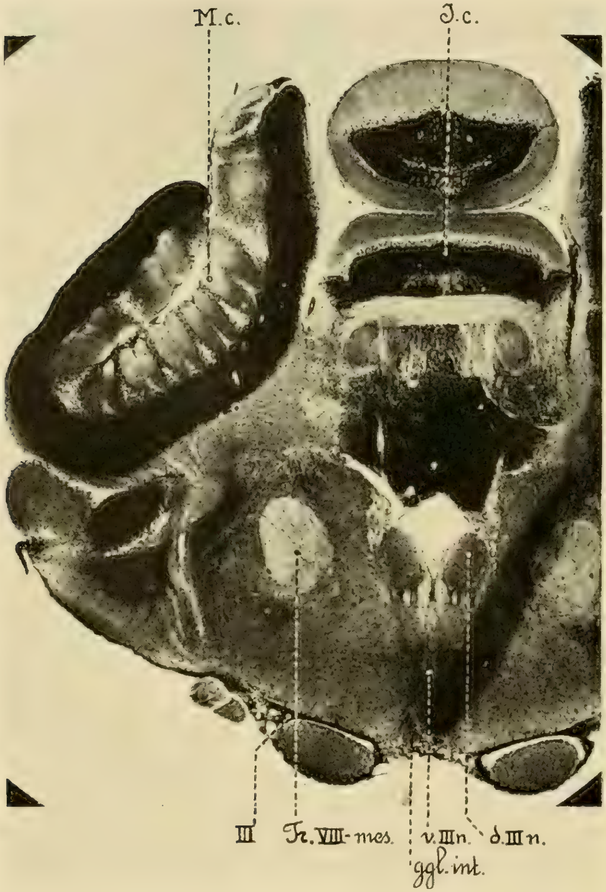


Fig 5.
Fig 6.
Fig 7.
Fig 8.
Fig 9.
Fig 10.
a
b.
c
N. lat. ant
VIII I
VIII II
N lat. post.
(1)
(2)
(3)
(4)
(5)
(6)
Nucl. centr. VIII
(7)
(8)
(9)
(10)
(11)
(12)
(13)
N. lat. post.

Figure 11



Figs. 12 to 19 A series of cross sections through the brain of Mormyrus caschive. The levels of figures 15 to 19 are indicated on figure 20.

Fig. 12 At the level of the III nucleus. *d.III n.*, nucleus dorsalis III; *ggl.int.*, ganglion interpedunculare; *I.c.*, Ichthyo-cerebellum; *III*, nervus oculomotorius; *M.c.*, Mormyro-cerebellum (Franz); *Tr.VIII mes.*, tractus octavo-mesencephalicus (lemniscus lateralis); *v.III n.*, nucleus ventralis III.

Fig. 13 At the level of the IV nucleus. *I.cer.*, Ichthyo-cerebellum; *III*, nervus oculomotorius going forward; *IV*, trochlear root at its exit; *IV n.*, trochlear nucleus; *IV r.*, trochlear root; *M.cer.*, Mormyro-cerebellum (Franz); *Tr.VIII m.*, tractus octavo-mesencephalicus (lemniscus lateralis).

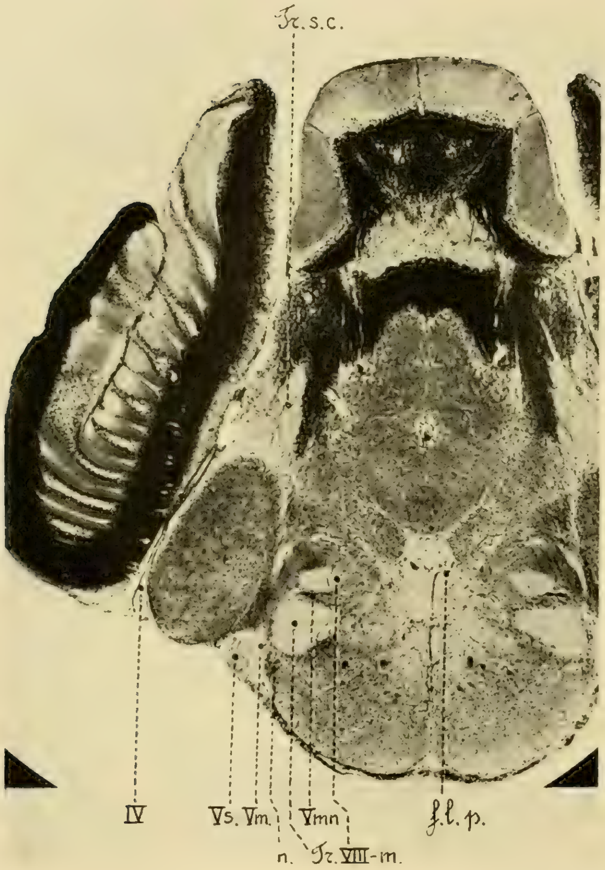


Fig. 14 At the level of the V roots. *f.l.p.*, fasciculus longitudinalis posterior; *IV*, nervus trochlearis; *n.*, nucleus at the side of the V roots at their entrance, consisting of some large cells; *Tr.s.c.*, tractus spino-cerebellaris; *Tr.VIII m.*, tractus octavo-mesencephalicus (Lemniscus lateralis or fasciculus longitudinalis lateralis) divided into two parts; *V m.*, motor V root; *V m.n.*, motor V nucleus; *V s.*, sensory V root.

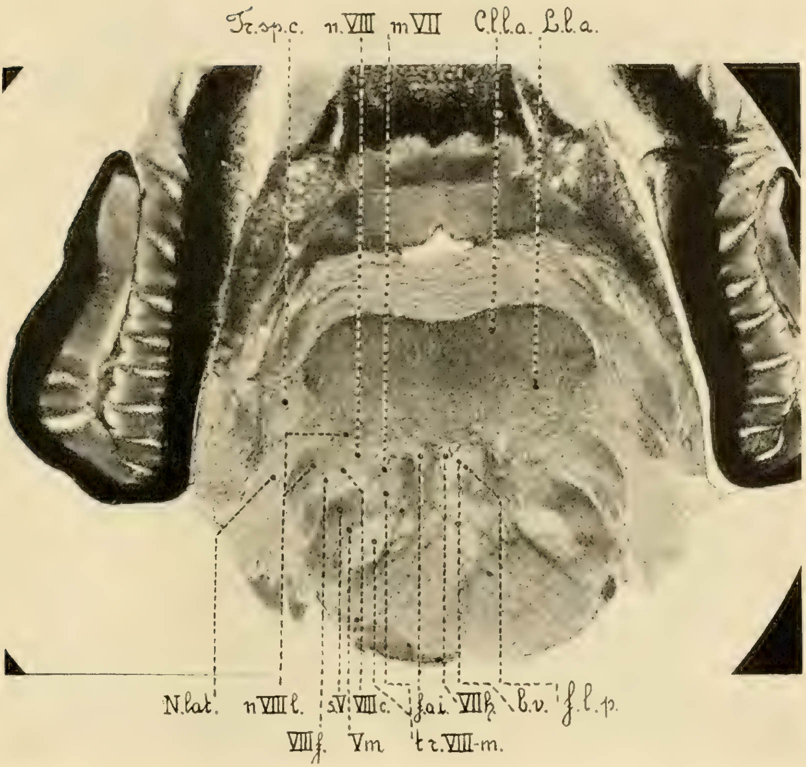


Fig. 15 At the level of the anterior lateralis root. *b.v.*, blood vessel; *C.l.l.a.*, crista lobi lateralis anterioris; *f.a.i.*, fibrae arcuatae internae; *f.l.p.*, fasciculus longitudinalis posterior; *L.l.a.*, lobus lateralis anterior; *m.VII*, ascending motor VII fibers near their frontal knee-bend; *N.lat.*, nervus lateralis anterior; *n.VIII*, nucleus of nervus vestibularis; *n.VIII l.*, lateral nucleus in which VIII fibers end; *s.V*, spinal V tract; *Tr.sp.c.*, tractus spino-cerebellaris; *tr.VIII m.*, tractus octavo-mesencephalicus; *V m.*, motor V root; *VII h.*, pars horizontalis of motor VII root; *VIII c.*, coarse fibers of VIII root [fig. 20 (5)]; *VIII f.*, fine fibers of VIII root, ascending to the gray matter of the nervus lateralis anterior [fig. 20 (6)].

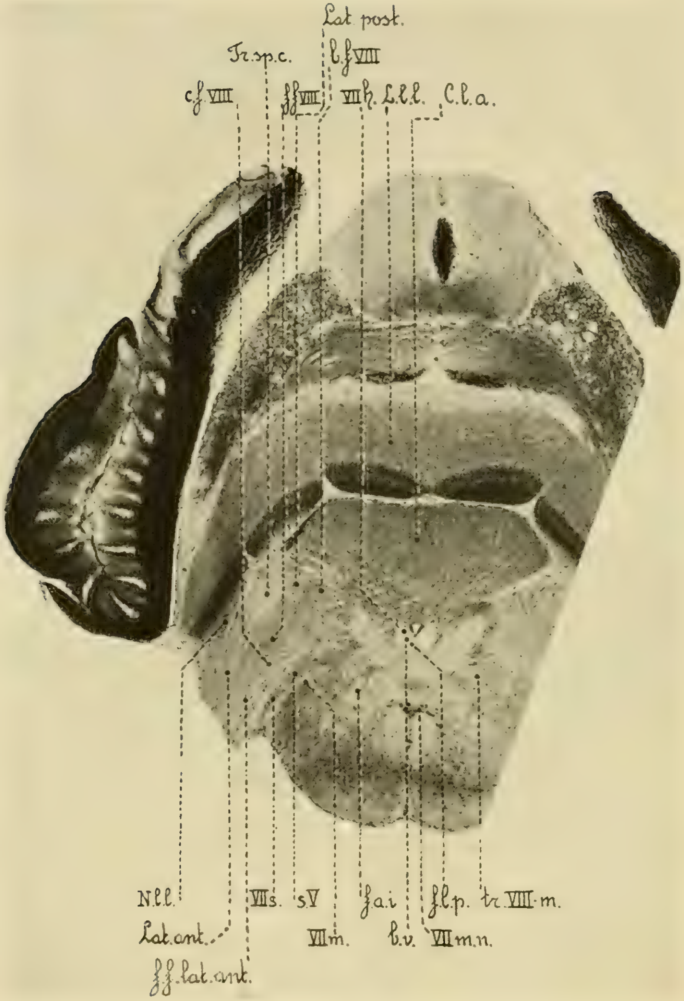


Fig. 16 At the level of the nervus lateralis anterior. *b.f.VIII*, fine fibers of VIII root, running backward after bifurcating; *b.v.*, typical blood vessel; *c.f.VIII*, coarse fibers of nervus vestibularis; *C.l.a.*, crista lobi lineae lateralis anterioris; *f.a.i.*, place where the fibrae arcuatae internae bend frontally, forming the fasciculus longitudinalis lateralis (*tr. VIII m.*); *f.f.lat.ant.*, fine fibers of nervus lateralis anterior; *f.f.VIII*, fine ascending fibers of VIII going forward [fig. 20 (6)]; *f.l.p.*, fasciculus longitudinalis posterior; *Lat.ant.*, fibers of nervus lateralis anterior ascending to the lobus lineae lateralis; *Lat.post.*, fibers of nervus lateralis posterior near their ending, after having pierced through the tractus spino-cerebellaris [fig. 20 (4)]; *L.l.l.*, lobus lineae lateralis; *N.l.l.*, nucleus lineae lateralis; *s.V*, spinal V tract; *Tr.sp.c.*, tractus spino-cerebellaris; *tr.VIII m.*, fibrae arcuatae internae turning forward to form the tractus octavo-mesencephalicus; *VII h.*, pars horizontalis of motor VII root; *VII m.*, motor VII root; *VII m.n.*, motor VII nucleus; *VII s.*, sensory VII root.

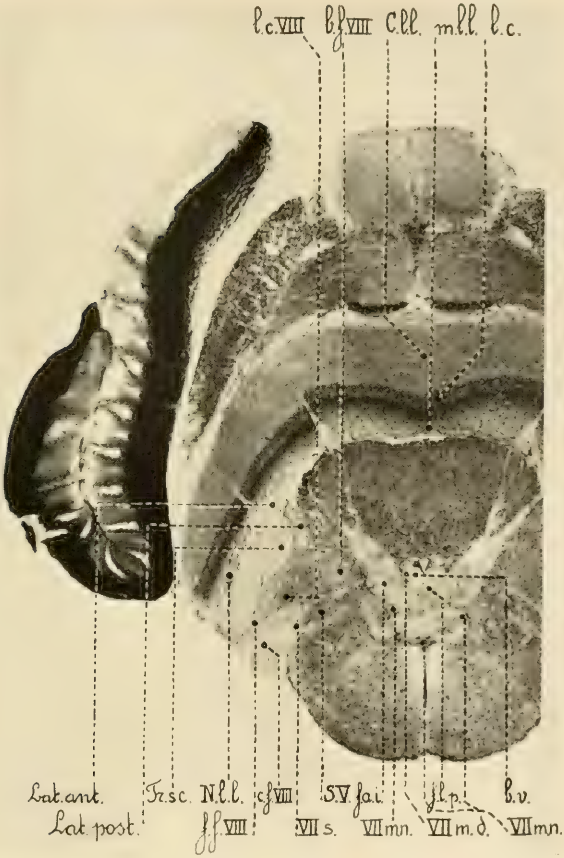


Fig. 17 At the level of the VIII roots. *b.f.VIII*, fine fibers of VIII nerve going backward after bifurcation; *b.v.*, blood vessel; *c.f.VIII*, coarse fibers of VIII root going forward; *C.l.l.*, crista lobi lineae lateralis; *f.a.i.*, fibrae arcuatae internae; *f.f.VIII*, fine fibers of VIII root at the level of their entrance approaching the gray matter of the lobus lineae lateralis anterioris; *f.l.p.*, fasciculus longitudinalis posterior; *Lat.ant.*, fibers of nervus lateralis anterior ending in the medulla of lobus lineae lateralis; *Lat.post.*, fibers of nervus lateralis posterior piercing the tractus spino-cerebellaris; *l.c.*, double layer of large cells on the granular layer of the lobus lineae lateralis; *l.c.VIII*, large cells belonging to the gray matter of VIII nerve; *m.l.l.*, medulla of lobus lineae lateralis; *N.l.l.*, nucleus lineae lateralis; *s.V*, spinal V tract; *Tr.s.c.*, tractus spino-cerebellaris; *VII m.d.*, descending part of motor VII root; *VII m.n.*, motor VII nucleus; *VII s.*, sensory VII root.

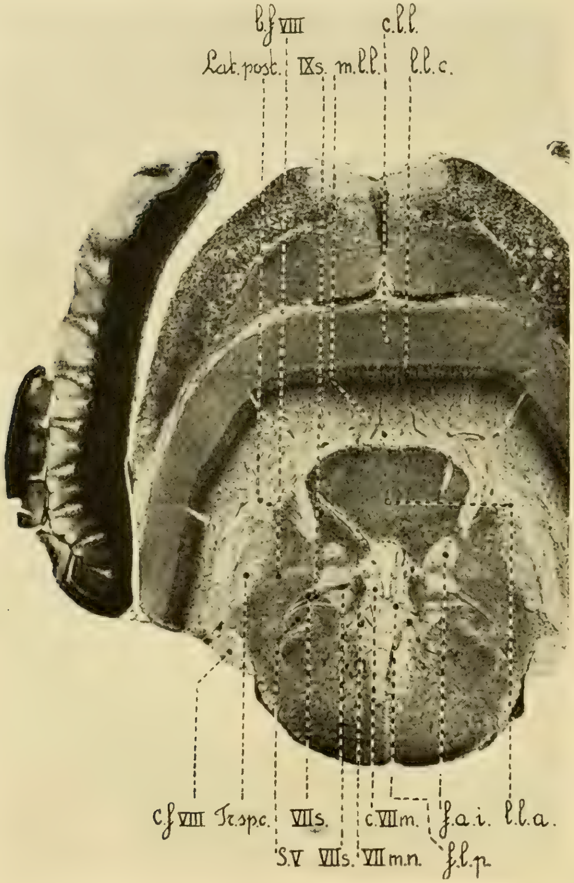


Fig. 18 A short distance in front of the IX roots. *b.f.VIII*, fine VIII fibers ending in the gray matter of the nervus lateralis anterior after bifurcation; *c.f.VIII* coarse fibers of VIII, *c.l.l.*, crista lobi lineae lateralis; *c.VII m.*, motor VII root directed caudad to VII–IX–X column; *f.a.i.*, fibrae arcuatae internae; *f.l.p.*, fasciculus longitudinalis posterior; *IX s.*, sensory IX root between two parts of the sensory VII root; *Lat.post.*, fibers of nervus lateralis posterior ascending directly into the medulla of the lobus lineae lateralis; *l.l.a.*, lobus lineae lateralis anterior; *l.l.c.*, double layer of large cells; *m.l.l.*, medulla of lobus lateralis; *s.V*, spinal V tract; *Tr.sp.c.*, tractus spino-cerebellaris with fibers of nervus lateralis posterior contained within it; *VII m.n.*, nucleus of motor VII root; *VII s.*, sensory VII root.

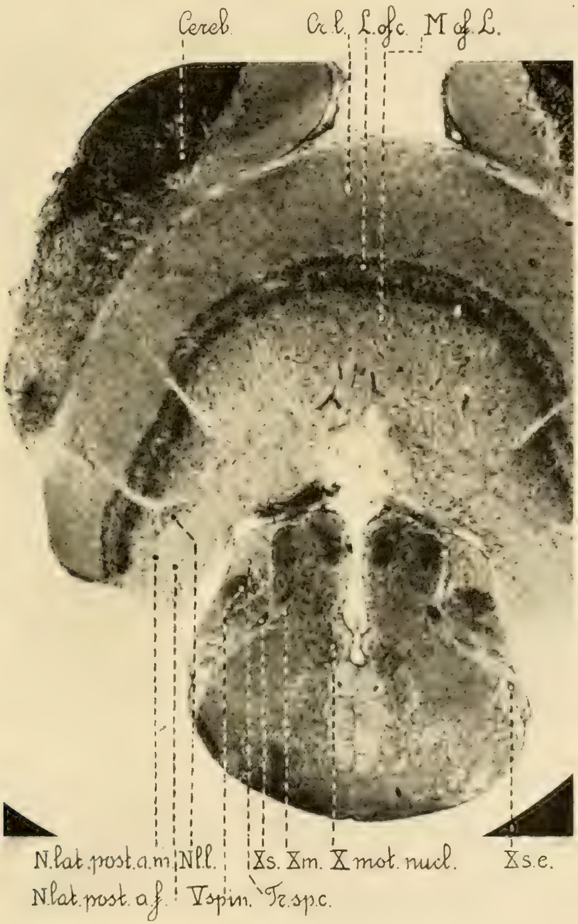


Fig. 19 At the level of the posterior lateralis root. *Cereb.*, cerebellum; *Cr.l.*, crista lobi lateralis; *L. of c.*, double layer of large cells; *M. of L.*, medulla of lobus lineae lateralis with granular cells; *N.lat.post.a.f.*, fibers of nervus lateralis posterior ascending frontally (after bifuraction?); *N.lat.post.a.m.*, fibers of nervus lateralis posterior ascending directly medially to the medulla of the lobus lineae lateralis; *N.l.l.*, nucleus lineae lateralis; *Tr.sp.c.*, tractus spino-cerebellaris; *V spin.*, spinal V tract; *X m.*, motor X root; *X mot.nucl.*, cells of the motor X column; *X s.*, sensory X root; *X s.e.*, exit of sensory X root.

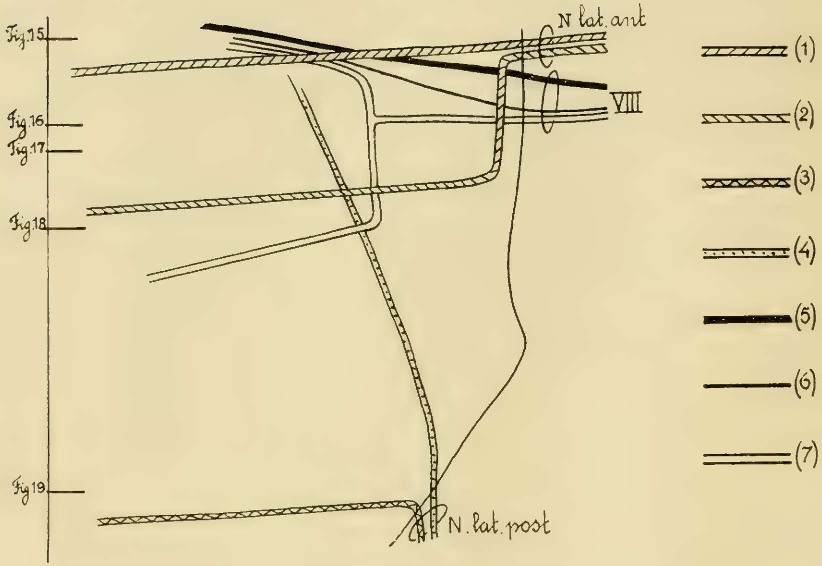


Fig. 20 Diagram of the relations of the VIII and lateralis roots of Mormyrus caschive; compare figures 12 to 19.

(1) direct fine fibers of nervus lateralis anterior ending in lobus lineae lateralis anterior.

(2) fine fibers of nervus lateralis anterior ending in lobus lineae lateralis (after bifurcation?).

(3) direct fibers of nervus lateralis posterior ending in lobus lineae lateralis.

(4) fibers of nervus lateralis posterior (after bifurcation?) ascending to ventro-lateral gray matter of lobus lineae lateralis anterioris.

(5) coarse fibers of VIII nerve ending beneath the gray matter of the nervus lateralis anterior.

(6) fine fibers of VIII nerve ending in the gray matter of nervus lateralis anterior and posterior (most frontal fine fibers).

(7) fine fibers of VIII nerve bifurcating, each part ending in the lobus lineae lateralis anterioris.

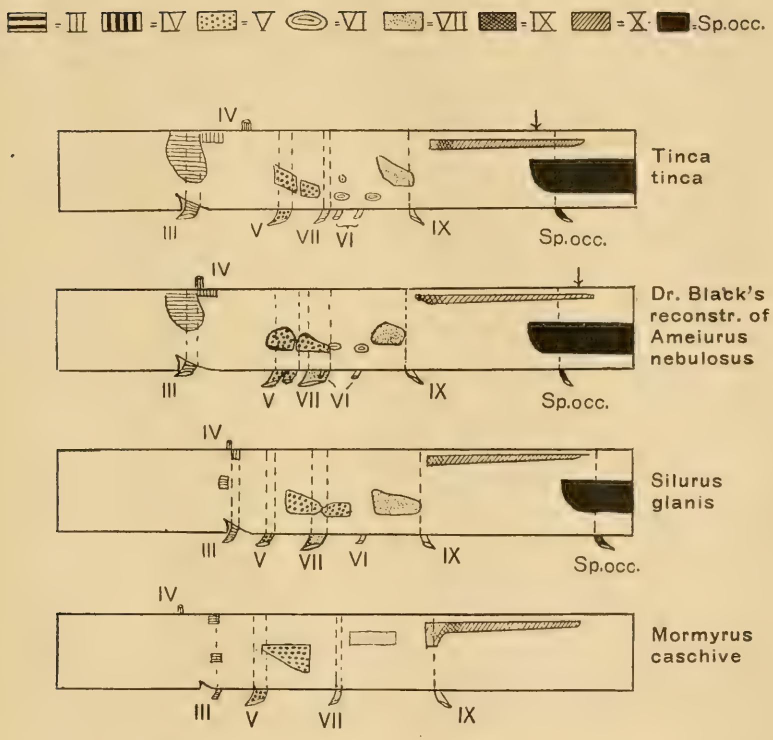


Fig. 21 Diagrams of the relations of the motor nerves and their nuclei in Tinca tinca (after Kappers), Ameiurus nebulosus (after unpublished researches of Davidson Black), Silurus glanis and Mormyrus caschive.

THE DEVELOPMENT OF REFLEX MECHANISMS IN AMBLYSTOMA

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From the Anatomical Laboratories of the University of Chicago and the University of Kansas

TEN FIGURES

The vertebrate nervous system consists very largely of reflex mechanisms of various grades of complexity with innumerable interrelationships, all of which are integrated by a system of higher correlation centers. In approaching the problem of the analysis of these mechanisms, we are accustomed to use the concept of a simple reflex arc (fig. 1) as our point of departure and to think of the more elaborate systems in terms of this type of unit. As a matter of pedagogic convenience, this method of procedure of course finds abundant justification; but if we consider the problem from the genetic standpoint, the question arises, whether this type of a simple two-neurone reflex arc represents the beginning or the end of the developmental sequence.

It is generally conceded that the earliest form of nervous system to appear in animal evolution was probably a diffuse system similar to that of the coelenterates and that the central nervous system of higher forms arose by a process of condensation within this diffuse nervous reticulum in the interest of the correlation and integration of the nervous control of the separate organs. A certain amount of such integration can be effected in a multicellular organism without the aid of any nervous system whatever, as illustrated by the sponges, by Volvox and by the higher plants; and nervous protoplasm appears to have been differentiated at first very gradually out of the protoplasmic strands concerned with this type of correlation.

We have a tolerably complete picture of the steps in the physiological development of the swimming reflex in response to external stimulation in the case of Diemyctylus and Amblystoma (Coghill, '09) and more recent anatomical work has revealed to us some of the details of the inter-neuronic connections involved in these reactions at successive stages of complexity. These ontogenetic studies are important in themselves in that they give an insight into the mechanism of functional differentiation, and it may be that they will also contribute something to our knowledge of the factors involved in phylogenetic differentiation.

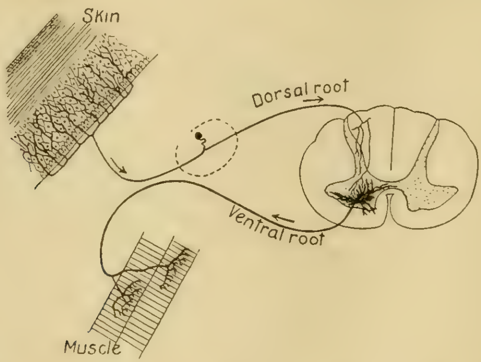


Fig. 1 Diagram of a simple reflex arc illustrated by a dorsal and a ventral root neurone of the spinal cord. After Van Gehuchten (slightly modified).

The Amphibia present peculiarly favorable materials for studies of this character, for the embryo becomes functional at a very early stage of differentiation, in this respect contrasting sharply with higher vertebrates, where organ formation and histogenesis are much further advanced before functional activity is possible. In amphibian larvae we are, therefore, able to watch the process of tissue differentiation during all of its later stages parallel with the correlated changes in behavior, and thus to avoid many pitfalls in the interpretation of the data. The steps in the ontogenetic development of the mechanisms of some typical reflexes of Amblystoma tigrinum will now be described.

THE EARLIEST SWIMMING REFLEX

It has been shown (Coghill, '09, '13, '14) that in Amblystoma the earliest somatic movements in response to external stimulation are possible only after the completion of a definite anatomical circuit in the nervous system (though the muscles may be excited to contraction by the direct application of an electrical stimulus prior to this age). The first movement which can be evoked by light tactile stimulation of the skin is a simple avoiding reaction—at first turning the head end of the body away from the side stimulated, then a convulsive 'coil reaction,' then an 'S-reaction,' which is immediately followed by a true swimming reflex.

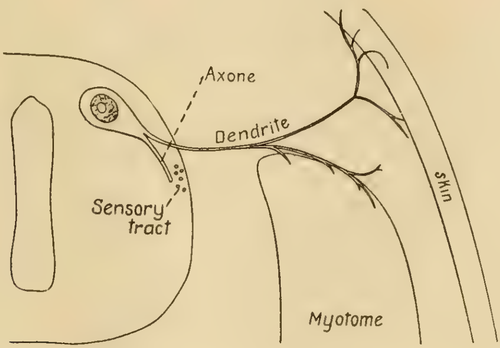


Fig. 2 Diagrammatic cross section through the body of an early swimming stage of larval Amblystoma, to illustrate the connections of the transitory giant cells of Rohon-Beard. Based on the researches of Coghill ('14).

During these periods the nervous system has the structure shown diagrammatically in figures 2 and 3, the peripheral sensory neurones lying within the spinal cord (the transitory dorsal giant cells of Rohon-Beard) and sending dendritic processes outward to both the skin and the myotomes. The axones of these cells ascend in a dorso-lateral sensory tract, whence they are discharged into a series of commissural cells, whose axones cross to the opposite side in the ventral commissure, after which they effect connection with cells of the descending motor tract.

The axones of the neurones last mentioned give off collaterals which form ventral root fibers and thus innervate the muscles (fig. 3).

In the youngest stages which are capable of responding at all to external stimuli, commissural fibers cross at one region only, viz., the upper end of the spinal cord and lower end of the medulla oblongata. In older stages, this ventral commissure is extended

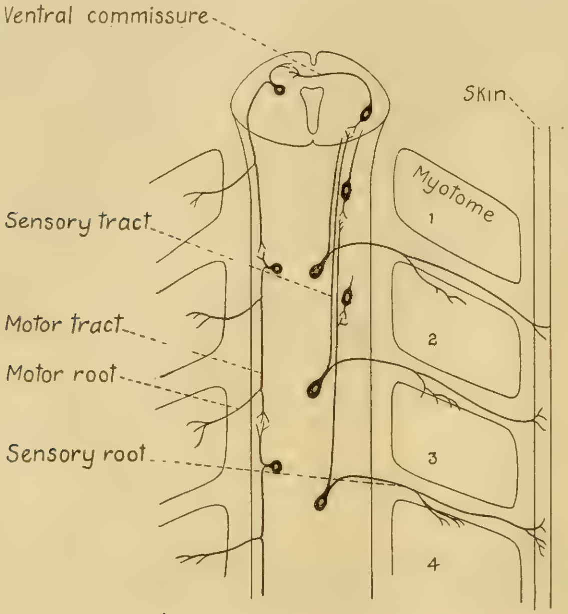


Fig. 3 Diagram of a dorsal view of the upper end of the spinal cord of larval Amblystoma of the same age as in figure 2, to illustrate the relations of the giant cells, commissural cells and motor cells and the mechanism of the swimming reflex. Based on the researches of Coghill ('13, '14).

both forward and backward from this level until finally it extends throughout the entire central nervous system below the optic chiasma, and other types of connection between the peripheral sensory and motor neurones are effected, so that local crossed and uncrossed reflexes are possible in every part of the central nervous system.

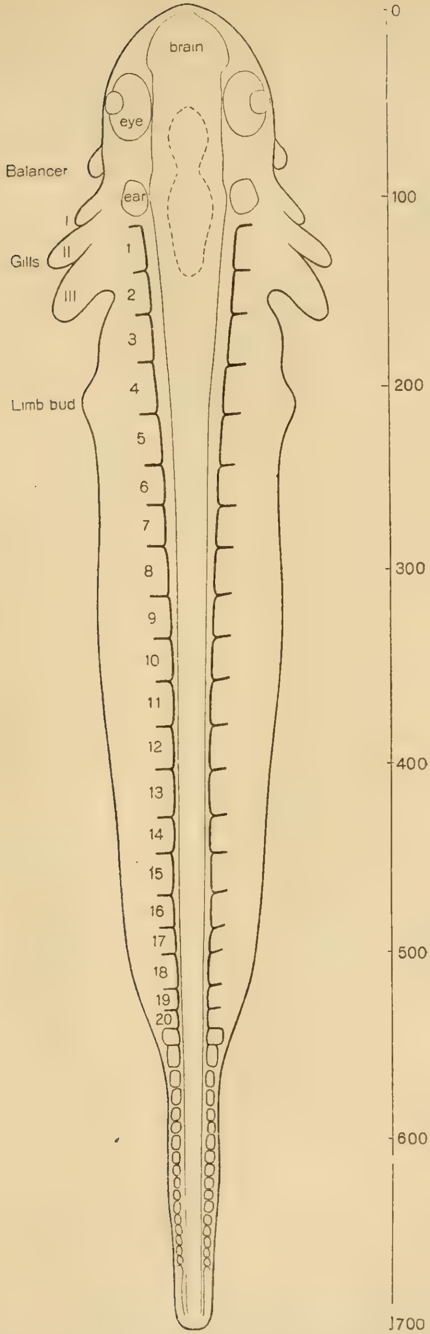
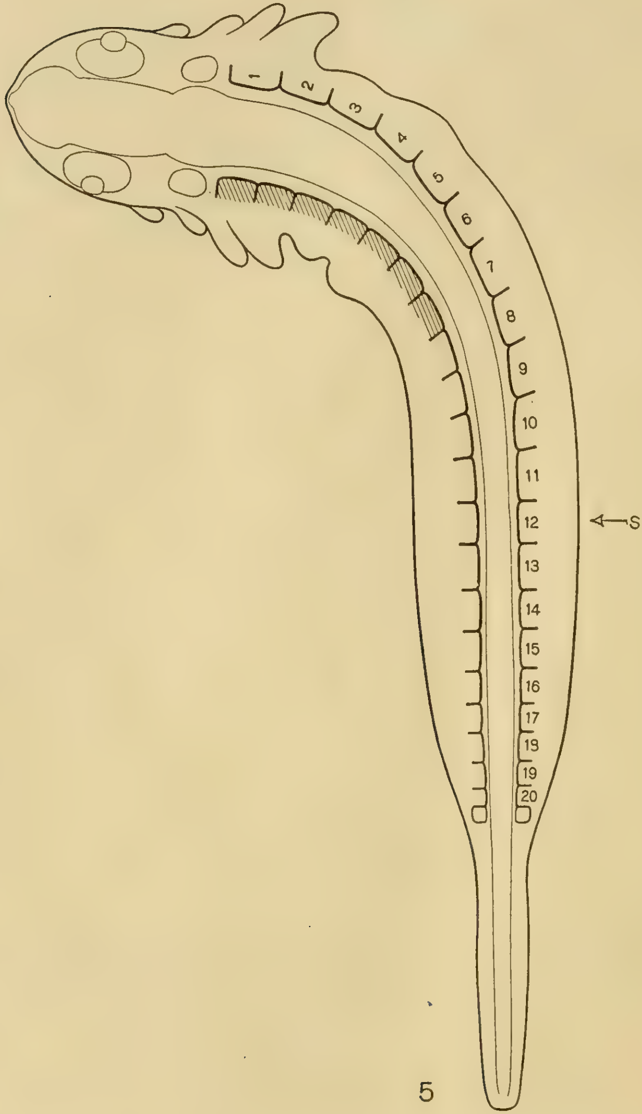


Fig. 4. A projection upon the horizontal plane of the central nervous system and myotomes of larval Amblystoma punctatum, early swimming stage. × 25. This projection is reconstructed to scale from transverse sections of 10 μ in thickness, the serial numbers of the sections being indicated at the right.



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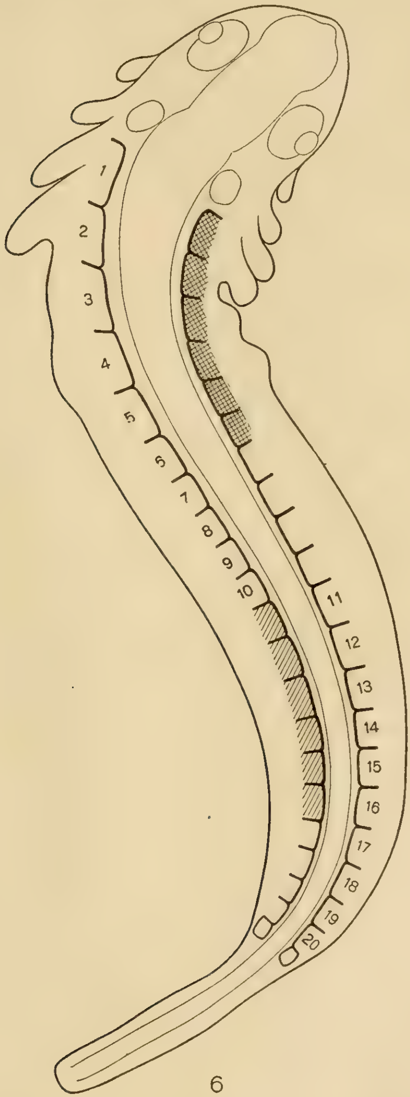
Figs. 5 and 6 Diagrams illustrating the contractions of the myotomes, resulting from the application of an external stimulus at *S* (fig. 5), in the first and second phases of the swimming reflex of an Amblystoma larva of the same age shown in figure 4. After the researches of Coghill ('09, '13, '14). The myotomes involved



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in the first contraction are cross-hatched with simple oblique lines; these at first are at the upper end of the body (as in fig. 4), while in the second phase this movement is farther back (fig. 5). In figure 5 the myotomes involved in the second contraction at the beginning of the second phase are double cross-hatched.

From these observations it follows that the earliest reflex responses to external stimulation require a rather complex chain of neurones, whose relations are quite different from those of the shortest definitive reflex arc of the adult animal.

In this arrangement we would emphasize the following features: (1) the fact that a single peripheral sensory neurone may be excited either by an exteroceptive stimulus applied to the skin or by a proprioceptive stimulus ('muscle sense') arising from the contraction of the myotome during the act of swimming; (2) the fact that the peripheral motor neurones are not yet separately differentiated away from those of the central motor tract; (3) that the reflex path required for the type of crossed reaction which is first to appear is a relatively long one, all of the afferent impulses having to reach the upper end of the spinal cord before they can be transferred across the mid-plane into the efferent apparatus; (4) that the individual neurones of this circuit are relatively short and that many synapses are interpolated in the pathway.

In the actual operation of this mechanism it appears that a somatic movement may be initiated by a single external tactile stimulus (say at *S*, fig. 5) which is transmitted inward through the cutaneous dendrite of a dorsal giant cell (figs. 2 and 3) and that this movement takes the form of a swimming reflex whose rhythm begins at the head end of the body and is transmitted backward through the myotomes of the side opposite to the one stimulated. The first stage in this movement is a bending of the head away from the side touched (fig. 5). This curvature of the body then moves backward, involving the successive contraction of additional myotomes, and after several myotomes of the upper part of the trunk have been involved, the muscular branches of the dorsal giant cells are excited by the contraction of their respective myotomes (myotomes 11 to 16 on the left side of fig. 6), thus exciting a proprioceptive reaction. This stimulus is likewise transmitted to the upper end of the spinal cord, passed over to the opposite side and into myotomes lying in front of those now in contraction (myotomes 1 to 6 on the right side of fig. 6). The effect is to turn the head to the opposite

side and thus initiate a descending wave of muscular contraction which follows the first but in the opposite direction. This process is continued and repeated as long as the swimming movement persists, thus giving rise to the serpentine swimming reflex.

This mechanism obviously is adapted to produce only one form of response to any sort of excitation applied to the trunk region of the embryo, viz., a swimming reaction, and the same neurones are involved throughout in both the exteroceptive and the proprioceptive factors in the reaction. Physiological experiments show that this in fact is the case.

At a later period in development the transitory dorsal giant cells disappear and are replaced by typical spinal ganglion neurones which have meanwhile differentiated from the neural crest. And no doubt the adult Amblystoma, like the higher vertebrates, possesses distinct neurones within the spinal ganglia to serve the exteroceptive and the proprioceptive functions respectively involved on the afferent side of the swimming reflex.

In older larvae the efferent side of the reflex circuit also shows an advance beyond that of the youngest swimming embryo, where the motor root fibers arise as collateral branches from the descending tract fibers. The details of the transformation have not been observed; but it is probable that in some of these neurones the descending tract fiber elongates and develops at the expense of the peripherally directed collaterals, while in others a collateral develops at the expense of the descending fiber, thus transforming the element into a typical ventral horn neurone.

SPINAL REFLEXES IN THE HALF GROWN LARVAE

The spinal cords of urodele larvae have been investigated histologically by several observers, the most important of these studies being those of van Gehuchten ('97) upon Salamandra. Most of his observations have been confirmed upon Amblystoma larvae and figure 7 presents a diagram which elucidates some of these relations. This mechanism is much more complex than that of the earliest swimming larva, though still very different from that known in the spinal cords of adult higher vertebrates.

The spinal ganglion cells and the ventral horn cells have fully matured and the figure shows that both crossed and uncrossed reflex connections are possible at all levels of the spinal cord. Dorsal root fibers from the spinal ganglion neurones pervade the dorsal part of the white substance and the remainder of this layer is filled with various kinds of correlation fibers. Both the correlation neurones and those of the ventral horns send enor-

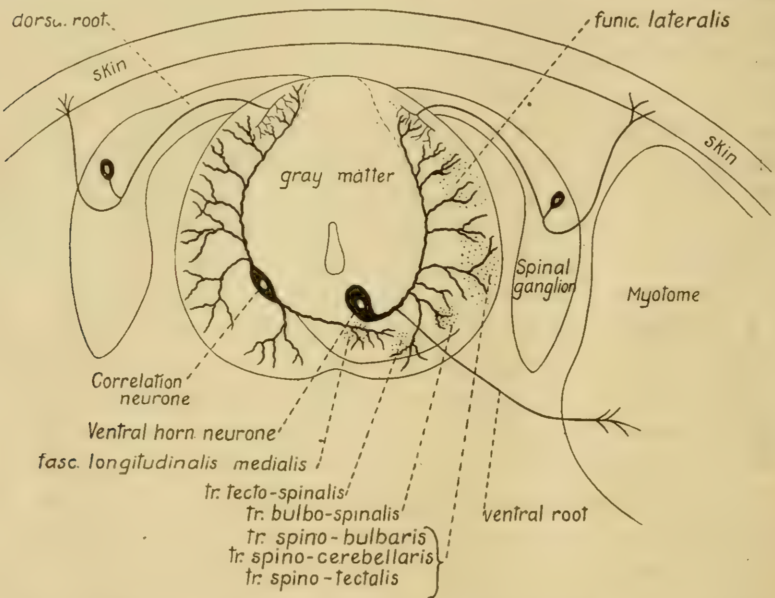


Fig. 7 Diagram of the relations of some of the neurones of the spinal cord of larval Amblystoma.

mous dendrites into all parts of the cross section of the white substance, some even crossing to the opposite side through the ventral commissure.

From these relations it is evident that each peripheral motor neurone is under the direct physiological influence of every sort of nervous excitation which can be transmitted through the spinal cord. These excitations may come from the skin of its own or of very remote segments of the body through dorsal root

fibers, or they may come from the brain through the various cerebro-spinal tracts—from the visual centers through the tractus tecto-spinalis, from the auditory or vestibular centers through the tractus bulbo-spinalis, etc. Furthermore, the long ascending systems between the spinal cord and the brain (spino-bulbar, spino-cerebellar and spino-tectal tracts) may also discharge collaterals among dendrites of these peripheral motor neurones.

The Amblystoma larva is capable of making only the simplest responses by means of the body musculature, of which the chief is the simple swimming movement; but, unlike the young embryos considered in the preceding section, these responses may be called forth by a great variety of means. The body musculature here is responsive to environmental influences received through many more avenues of sense, and its movements are, in addition, under the control of the higher correlation centers of the brain.

THE MAMMALIAN SPINAL CORD

The mechanism of mammalian spinal reflexes need not be here reviewed, especially since our present knowledge of the subject has been so admirably summarized by Sherrington ('06). The most significant feature here from our present standpoint is the further advance in the differentiation of the effector apparatus.

Though the spinal cord of larval Amblystoma may be excited by means of a wide range of receptors, the typical response is a total reaction of essentially the same sort in all cases. In mammals the differentiation of the limbs and other highly special motor organs permits of an extensive series of refined movements; and in conformity with this diversity of response we find the correlation neurones of the spinal cord organized into elaborate functional systems, each of which may act either independently or conjointly with others upon particular groups of synergic motor neurones. The cord of larval Amblystoma may be conceived as a house with many entrances and but one exit; that of a mammal with still more entrances and also a large number of exits.

THE MEDULLA OBLONGATA OF LARVAL AMBLYSTOMA

The medulla oblongata and cranial nerve roots of half grown larvae of Amblystoma have recently been analyzed (Herrick, '14), and some very interesting relations have come to light. The functional components of the roots and peripheral branches of the cranial nerves of old larvae and adults of Amblystoma tigrinum have been previously analyzed by Coghill ('01, '02) and the more recent observations of Herrick show that in younger larvae essentially the same functional pattern is present in the nerve roots as in the older specimens described by Coghill. It is necessary therefore here merely to call attention to the fact that the components of the cranial nerve roots in the half grown larvae here under consideration conform in all respects to the arrangement which is characteristic of the adult forms of the Ichthyopsida in general, as elucidated in a large number of species by recent students of nerve components.

This implies that each physiological type of peripheral end-organs has its own distinct ganglia and nerve roots in the medulla oblongata. The nerves of general sensibility enter the brain through the V, X and probably the VII roots and pass into the spinal V root. The nerves of general visceral sensibility and taste enter by the VII, IX and X roots and pass into the fasciculus solitarius. The fibers from the internal ear (VIII root) enter a longitudinal tract lying immediately dorsally of the spinal V tract; those of the lateral line X roots enter two similar tracts lying farther dorsally; and those of the lateral line VII roots enter three such tracts, one between the two lateralis X roots and two above the dorsal lateralis X root.

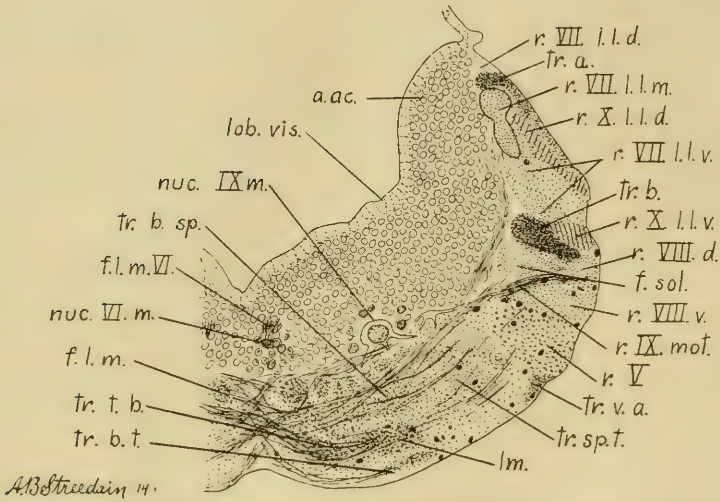
Each root fiber of all of these components, without exception, immediately upon entering the medulla oblongata divides into ascending and descending branches which pass respectively upward and downward for long distances, thus forming the tracts of root fibers to which reference has just been made. These root bundles extend through practically the entire length of the medulla oblongata, maintaining throughout the same relations to each other, so that cross sections through all parts of the medulla

oblongata, except the extreme caudal end, show essentially the same pattern of functional localization of peripheral sensory root fibers.

A typical section through the middle of the oblongata is shown in figure 8, and the ensemble of these roots as projected upon the lateral surface of the oblongata is indicated diagrammatically in figure 9.

The bundles of sensory root fibers, as shown by figure 8, make up most of the white substance of the dorsal half of the medulla oblongata, save for two strong correlation tracts (*tr.a* and *tr.b.*). The ventral half of the white substance contains the motor roots (a ventro-lateral visceral series and a ventro-medial somatic series) and numerous long correlation tracts between the oblongata and other parts of the central nervous system.

In these larvae the peripheral sensory and the peripheral motor neurones appear to be as clearly differentiated into distinct functional systems, each with its own type of highly specialized end-organ, as in higher vertebrates; and indeed the arrangement of these functional systems in the cranial nerve roots is essentially similar throughout the vertebrate series. But the central correlation neurones by which these peripheral elements are put into physiological connection exhibit here an arrangement which, so far as hitherto described, is unique among the vertebrates. The specificity of function which is so characteristic of the peripheral neurones is here no longer in evidence, except in a very general way. This is illustrated by the relations shown in figure 10. The neurone shown on the right side of this figure sends one main dendrite downward into the spinal V tract, where it engages collaterals from root fibers of the general cutaneous system. Another main dendrite passes laterally into the fasciculus solitarius, where it engages collaterals from the gustatory and other visceral sensory root fibers which compose this fasciculus. The axone of this neurone may enter the uncrossed secondary visceral tract (*tr.v.a.*), or it may decussate to enter a crossed ascending path (*tr.b.t.*), or in some cases it appears to divide and send a branch into each of these tracts, as shown in the figure. The left side of figure 10 illustrates a neurone lying a



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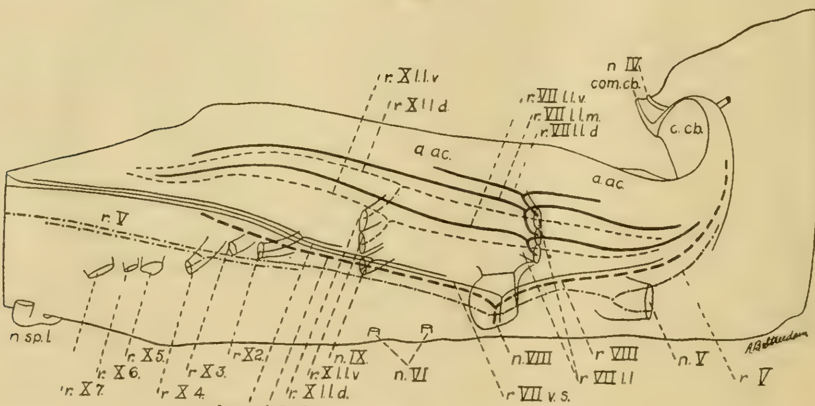

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Fig. 8 Cross section through the right half at the medulla oblongata near the roots of the IX cranial nerve of a 38 mm. larva of Amblystoma tigrinum (from Herrick, '14, fig. 14).

Fig. 9 View of a wax model of the medulla oblongata of the same specimen of Amblystoma from which figure 8 was taken, seen from the right side. × 42 (from Herrick, '14, fig. 3). The entire intra-medullary course of a single typical fiber of each sensory component of the cranial nerve roots is shown as projected upon the lateral surface. The general cutaneous fibers are shown in dot and dash lines; the VIII fibers in heavy broken lines; the visceral sensory fibers in thin continuous lines; the lateral line X roots in thin broken lines; the lateral line VII fibers in thick continuous lines.

little farther dorsally in the acustico-lateral area. Its dendrites may reach the root zone of the lateral line root of the vagus, of the VIII root, of the spinal V tract, and even farther ventrally into the tegmentum, where it may receive collaterals from the spino-bulbar and spino-tectal paths. The axone of this neurone enters the lateral lemniscus (*lm.*) for connections with the midbrain and thalamus.

The relations of these nerve centers in adult Amblystoma have been only superficially studied. There is undoubtedly some advance in specialization over the larval condition, but apparently no fundamental changes in reflex pattern. Further research is needed to clarify the details of this situation in the adult.

REFERENCE LETTERS

for figures 8, 9 and 10

a.ac., area acustico-lateralis
c.cb., corpus cerebelli
com.cb., commissura cerebelli (medullated component)
f.l.m., fasciculus longitudinalis medialis
f.l.m.VI., tract from area acustico-lateralis to VI nucleus
f.sol., fasciculus solitarius
gen.cut.X., general cutaneous root of vagus
l.l.X., radix lateralis vagi
lm., bulbar lemniscus (from area acustico-lateralis)
lob.vis., lobus visceralis
n.IV., nervus trochlearis
N.IX., nervus glossopharyngeus
n.sp.1., first spinal nerve
nuc.IX.m., nucleus motorius IX
nuc.VI.m., nucleus motorius VI
n.V., nervus trigeminus
n.VI., nervus abducens
n.VIII., nervus acusticus
r.IX.mot., radix motorius IX
r.V., sensory root of the V nerve
r.VII.l.l., radix lateralis facialis
r.VII.l.l.d., radix lateralis facialis dorsalis
r.VII.l.l.m., radix lateralis facialis medius
r.VII.l.l.v., radix lateralis facialis ventralis
r.VII.v.s., visceral sensory root of the facialis
r.VIII., radix nervi acustici
r.VIII.d., radix dorsalis acustici
r.VIII.v., radix ventralis acustici
r.X.l.l.d., radix lateralis vagi dorsalis
r.X.l.l.v., radix lateralis vagi ventralis
r.X.2 to r.X.7, second to seventh roots of the vagus
tr.a., dorsal longitudinal tract of area acustica
tr.b., ventral longitudinal tract of area acustica
tr.b.sp., tractus bulbo-spinalis
tr.b.t., tractus bulbo-tectalis
tr.sp.t., tractus spino-tectalis
tr.t.b., tractus tecto-bulbaris
tr.v.a., tractus visceralis ascendens (secondary gustatory tract)
Visc.sens.X., visceral sensory root of vagus

It is evident that the arrangement above described provides for the entrance into the medulla oblongata of sensory impulses of very specific sorts which are segregated physiologically into distinct roots and each functional system has its own area of distribution into the secondary centers. But, on the other hand, the arrangment of the secondary neurones is such that they can transmit these distinct physiological systems in separate form

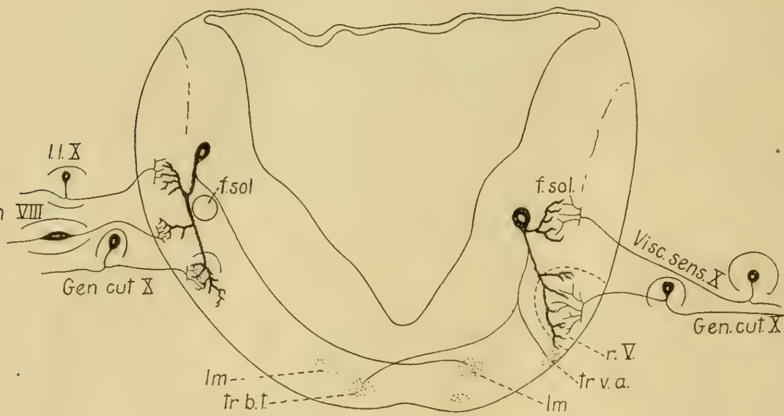

Fig. 10 Diagrammatic cross section through the medulla oblongata of larval Amblystoma of the same age as figures 8 and 9, to illustrate types of connections of the secondary sensory neurones. The relations shown on the right side can be seen in a single section (cf. Herrick, '14, figs. 38, 39, 40). The left side is a composite picture based on sections of different levels somewhat farther rostrad than the level shown on the right (cf. Herrick, '14, figs. 34, 35, 36). For reference letters, see page 79.

into the secondary correlation tracts only imperfectly, so that each of these correlation tracts may be actuated physiologically at the same time by two or more diverse physiological systems of the periphery—in the one case by both gustatory and tactual stimuli and in the other case by stimuli received from lateral line, vestibular (or auditory) and tactile organs. Before considering the significance of these facts further, let us compare the corresponding mechanisms of the mammalian brain.

THE MEDULLA OBLONGATA OF MAMMALS

Here the arrangement of receptors and peripheral sensory nerve components is in all essential respects the same as in the urodele Amphibia. It is true that some details of the pattern have been altered—the lateral line system has vanished, the cochlea has been added to the internal ear, etc.—but the general morphological pattern is the same, so far as the peripheral neurones are concerned. But after the first synapse has been passed the sensory neurones of the second order also are found to be segregated into definite sensory centers, each related exclusively to one peripheral system—the general cutaneous nerves all terminate in the gelatinous substance of Rolando or other gray matter related exclusively to the nerves of this functional system; the visceral sensory and gustatory nerves all terminate in the nucleus of the fasciculus solitarius, whose neurones receive stimuli from no other important sources; the vestibular and cochlear nerves terminate in their respective nuclei. Each of these sensory centers constitutes a specific 'nucleus,' differentiated away from the primordial central gray, which in Amblystoma preserves its original generalized character to a large extent. The secondary pathways leading away from these sensory nuclei may in mammals be as specific functionally as are the peripheral nerve roots which enter them, the correlation of these elements into particular reflex systems being accomplished in other centers farther removed from the primary afferent neurones.

Recurring to our analogy of a house with many doors, the medulla oblongata of larval Amblystoma may be compared with a building containing a large central hall, admittance to which may be gained from the outside through many doors; and leading out from the main hall is a smaller number of short, wide corridors some of which lead directly to exits, others to a common living room in another part of the dwelling. The mammalian medulla oblongata, however, is more like a large apartment building, composed of many suites, each with its separate entrance and exit, but the inner rooms of all having free communi-

cation from suite to suite and also with a series of large common living rooms. Here the individual suites would correspond with the separate reflex circuits and the common living rooms to the higher correlation centers.

CONCLUSION

The general results of this inquiry may now be briefly summarized and discussed.

The first response which the Amblystoma embryo can make to external stimulation of the skin is a simple avoiding reaction, turning the head away from the side touched. This is soon followed by an S-shaped reaction of the whole body, and this in turn by a simple swimming reaction. In the earliest stages of all of these reactions the afferent nervous impulse is transmitted through a chain of several neurones to the upper end of the spinal cord, thence across the ventral commissure into a descending efferent or motor tract, which is also composed of a chain of neurones. In the earliest swimmers the initial response, excited by cutaneous stimulation, is supplemented by a proprioceptive 'muscle-sense' response excited by the muscular contraction itself, and thus the rhythm of serpentine locomotion is maintained (figs. 5 and 6). At this age the same peripheral sensory neurone may serve both as exterceptor and as proprioceptor (figs. 2 and 3) and on the efferent side of the arc there is also a lack of differentiation between the tract neurones and the peripheral motor neurones (fig. 3). The only possible reaction to stimulation is a total response of the somatic musculature—the swimming reaction.

In the spinal cord of the half grown larva the simple peripheral sensory neurones of the earliest stage have been replaced by definitive spinal ganglion neurones, among which those concerned with exteroceptive responses are probably distinct from those involved in proprioceptive reactions. Long ascending and long descending tracts are differentiated within the spinal cord and peripheral motor neurones are now distinct from those of the long descending motor tracts. By the elimination of numerous synapses, conduction in the spinal cord is much more rapid

than in the younger embryos of the first reacting stages. In addition to these long paths, short reflex connections are now possible within a single segment of the cord. Nevertheless the dendrites of both individual correlation neurones and motor neurones reach all parts of the white substance, so that whatever the source of the stimulus a common type of total response habitually follows, as in the younger specimens—a simple swimming reflex.

The mammalian spinal cord shows a much more complete differentiation of individual reflex systems and a more perfect isolation of the long conduction pathways.

In the medulla oblongata of the half grown larva the peripheral sensory neurones show a high degree of functional specificity, and the central neurones of the second order tend to be grouped around these special sensory roots. But the functional localization of these secondary centers is not complete, each neurone having a dominant relation to some particular system of root fibers but also subsidiary connections with other functionally distinct systems of root fibers. Thus each primary bulbar center reached by terminals of sensory root fibers is also to some extent a correlation center, the secondary tracts are all of mixed function, and the analysis of function in the reactions is still incomplete. The peripheral sensory neurones, though segregated into functional systems as distinctly as in the cranial nerves of higher vertebrates and much more so than in the spinal nerves of any forms, are similar to those of the spinal nerves in that each fiber centrally reaches practically the entire length of the oblongata, giving to the primary sensory centers a longitudinal columnar arrangement which is apparently much more primitive than the more condensed sensory nuclei of mammals.

In the mammals the functional differentiation of the primary bulbar centers is complete and the functions of correlation are transferred to higher cerebral centers. Simpler total reactions of the more primitive sort are, however, still provided for in the reticular formation of the oblongata in these higher brains.

Throughout this series of forms of reflex connections we find a progressive differentiation of the specific reflexes away from the

type of total reaction and the gradual perfection of a great variety of individual adaptive movements, for each of which a particular chain of neurones is set apart. Rapid conduction through each of these circuits is then facilitated by the elimination of unnecessary synapses and the closer articulation of the residual neurones. From this it follows that the 'typical' two-neurone, short-circuit connection between dorsal and ventral root fibers, as illustrated by figure 1, appears late in development and is not to be regarded as a primitive form. In fact, all of the long correlation pathways of the central nervous system appear to develop relatively late in the ontogeny out of more complex chains composed of many more neuronic units. In this connection one is reminded that in the human brain the longest path of all, the pyramidal tract, is one of the last to mature.

How far the embryological sequence shown in the development of these pathways in the amphibian brain should be interpreted as evidence of the phylogenetic sequence, it would at present be premature to affirm positively. But it seems probable to us that the relations found in amphibian larvae are in many respects primitive; and this is in accord with the known form of connection of the nervous elements in the simplest types of nervous system and with the prevailing belief that every form of central nervous system has arisen by the concentration of an originally diffuse and relatively equipotential peripheral ganglionated plexus in the interest of an integration of all bodily functions. Parallel with this integrative process there was a progressive individuation of particular reflex circuits and their segregation out of the primordial general nervous matrix. Special correlation centers must then be developed in order that the primary integrative action of the nervous system may not be impaired in this process of individuation of its parts; and the more complex the particular functions of the parts, the more important become the correlation centers. Thus arose the great suprasegmental apparatuses (cerebellar and cerebral cortex) superposed upon the more ancient reflex systems of the brain stem.

Finally, we would urge that the factors operating in either the ontogenetic or the phylogenetic differentiation of the func-

tional mechanisms of the brain cannot profitably be investigated without a precise knowledge in each stage investigated of the peripheral relations of each of these functional systems and of the interrelations of the neurones involved at every step in the progress of the nervous impulse from periphery to center and back to the effector organs during the normal course of functional activity.

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MAUTHNER'S CELL AND THE NUCLEUS MOTORIUS TEGMENTI

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From the Anatomical Laboratory of the University of Chicago

THIRTEEN FIGURES

CONTENTS

INTRODUCTION. MATERIAL AND METHODS

This paper is part of an analysis of the central connections of the acoustico-lateral system in teleosts, undertaken at the suggestion of Prof. C. J. Herrick. Certain findings upon Mauthner's cell of more general interest than the discussion of the eighth and lateral line nuclei warrant the separation of this part of the work.

In 1882 Mayser wrote of Mauthner's cell: "Wenn irgend ein Theil des Fishgehirns, scheint mir dieses sonderbare Gebilde die Aufmerksamkeit der Histologen zu verdienen." Beccari ('07) published the first thorough study of this giant among nerve cells and I am adding futher details which it is hoped may serve as a basis for a physiological-histological investigation of its remarkable synapses and the constituents of its protoplasm. Furthermore, the relationship between Mauthner's cell, the Müller cells and the nucleus motorius tegmenti here elaborated may serve to clear up the nature of Mauthner's cell and its striking connections.

These observations are based chiefly upon the study of serial sections of the brains of Ameiurus and other teleosts, both larval and adult, prepared as follows:

10 series of Ameiurus, fixed with formol-Zenker and stained with toluidin blue and erythrosin;

20 series of Ameiurus, Cajal and Bielchowsky methods;

10 series of Ameiurus, fixed with formol-osmic-Zenker and acetic-osmic-bichromate, stained with iron hematoxylin;

10 series of larval trout heads, prepared chiefly by the Cajal method;

100 series of brains of siluroids and cyprinoids prepared by the Golgi method;

3 series of Ameiurus, Weigert method.

The brains prepared by the methods of Golgi and Weigert were loaned to me by Professor Herrick, who also placed at my disposal other series of brain sections, including representatives of various species of teleosts in addition to those mentioned above.

The toluidin blue and erythrosin method was found to be very certain in its results and particularly valuable in giving clear pictures of cell groups and fiber tracts, as well as showing the Nissl substance in the cells (figs. 3–9). The fish were decapitated and bled and the brains dissected out under a binocular microscope in normal salt solution. They were fixed in formol-Zenker for 2 to 12 hours according to their size, cut in paraffin 10 μ thick and stained in a 1 per cent solution of toluidin blue in water for 12 to 24 hours. The slide was then drained and dipped directly into a 0.5 per cent solution of erythrosin in 95 per cent alcohol and agitated until the sections were red. They were then dehydrated rapidly in absolute alcohol, cleared in toluol and mounted in neutral balsam.

Under the stimulus of the striking preparations of teleostean brains figured by Beccari ('07) and Tello ('09) I made many experiments with the Cajal method and elaborated a technique which is sure to give results with larval brains. Only about 10 per cent of the young adult brains gave preparations that were first rate, but 90 per cent were worth study. The following procedure may be recommended:

Fix entire heads of larvae or the brains of adults in acetic alcohol, varying the proportion of acetic acid according to the water

content of the brains, thus reducing the shrinkage of the cells without materially injuring the impregnation. This variation of acetic acid may be from 5 to 10 per cent. Larval Ameiurus and Salmo gave the best results with this mixture:

Absolute alcohol	10 parts
Glacial acetic acid	1 part

For adult Ameiurus both of the following fixing fluids gave good results in many cases:

Absolute alcohol	19 parts
Glacial acetic acid	1 part
or	
Absolute alcohol	19 parts
Glacial acetic acid	2 parts
Chloroform	10 parts

Twenty minutes is usually sufficient for fixation, though the brains may be left for $1\frac{1}{2}$ hours without becoming too brittle to cut. They are then rinsed in 80 per cent alcohol followed by distilled water and placed in a solution of silver nitrate. The penetration of the silver is the most important factor and this is facilitated by changing the strength of the solution daily and by keeping the material in an incubator. The material is put into 0.5 per cent silver nitrate and kept in the dark at a temperature of 35 to 40°C. for 24 hours, then washed in distilled water 5 minutes and put into a 1 per cent solution of silver nitrate. On the following day this is again changed to a 1.5 per cent solution, then to 2 per cent, then back to 1 per cent and the process repeated. The silver bath should not be stronger than 2 per cent, and the silver treatment should last not less than 3 days nor more than 8 days. Cells and their processes are usually best shown in preparations left in the silver for from 4 to 5 days, but in any case the material must be brown at the end of this treatment. It is then rinsed in distilled water and developed for from 12 to 24 hours in a 1 per cent solution of pyrogallol in 5 per cent neutral formol. It is then rinsed in distilled water, followed by 50 per cent alcohol, rapidly dehydrated in two changes of 95 per cent alcohol and of absolute alcohol, cleared in cedar

oil or bergamot oil and embedded in paraffin. The dehydration, clearing and embedding should not occupy more than 6 hours. The sections are cut from 6 μ to 10 μ thick and are best cleared in benzole. Entire heads of larvae prepared in this way showed some cells in every nucleus stained with all their processes, including the axone, and in many of them the endings of the fibers of the VIII nerve in the internal ear were perfect. The thin sections necessitate the cutting of many series in planes dictated by the direction of the fibers to be studied.

Some of the clearest pictures of the synapses of Mauthner's cell were obtained by a procedure that has not been used before on this material (figs. 11–13). Brains were fixed in the mixture recommended by Maximow ('09):

Zenker's stock solution (without acetic acid)	8 parts
40 per cent formaldehyde solution neutralized with $MgCO_3$	1 part
2 per cent aqueous solution of osmic acid	1 part

Fix for 6 to 18 hours, renewing the solution after the first 3 hours. Cut in paraffin 4 μ to 8 μ thick and stain with iron hematoxylin. By this means the cells and their most delicate processes are preserved with a minimum of shrinkage. In addition the myelin sheaths are blackened, and thus a series of larval brains of different ages gives an account of the order of myelination of the fiber tracts, an invaluable aid in the analysis of the tracts in so complicated a region of the brain as the anterior end of the oblongata.

It is a pleasure to acknowledge my indebtedness to Professor Herrick for his help and advice and to the other members of this department for their coöperation. The larval trout material was obtained through the courtesy of Dr. Raymond C. Osburn at the New York Aquarium and worked up in the laboratory of Prof. C. L. Bristol of New York University. I wish to thank both gentlemen for their help.

THE NUCLEUS MOTORIUS TEGMENTI

The term nucleus motorius tegmenti is here used to designate the column of cells which lies in the ventro-medial region of the medulla oblongata and is identical with the bulbar portion of this nucleus as defined by Edinger. It extends throughout the medulla oblongata and, with the abducent nucleus, constitutes the somatic motor column of the bulb. The following account is not intended to be complete but aims merely to present certain facts concerning the character of the cells, their grouping and the functional connections of the groups, in order that the relations of the cells of Mauthner and Müller to the nucleus may be clearly discussed. These giant cells are highly differentiated, but none the less integral members of the nucleus, which for the sake of clearness are discussed separately.

The extent and subdivisions of the nucleus may be seen in the horizontal projection drawn in figure 2, where it is indicated by the double cross-hatching. It will be noted that the four rostral groups (*P.Supa.*, *P.Sup.*, *P.Pre. M.*, *P.Post M.*) are roughly co-extensive with the motor Vth nucleus; the caudal end of the pars postmauthnerea (*P.Post M.*) and a small group which is not indicated are similarly related to the two small VIth nuclei; the pars intermedia (*P. Int.*) and the pars inferior (*N.Mot.Teg.Inf.*), coincide less obviously with the motor VIIth and nucleus ambiguus respectively. This chart is based upon projections of the adult brain; in larvae the groups are more widely separated and their relations to the motor nuclei are more clearly marked. The latter relation is no doubt the primitive one, i.e., the nucleus serves to coördinate the activities of the motor nuclei of the brain and cord. Secondarily other connections have been established with primary sensory centers of the oblongata and these connections are physiologically the more important ones, as will be seen below.

The position of the nucleus in the cross section is shown in figure 4 at *P.Post M.* and in figure 5 at *N.mot.tegm.*, where it is seen to be made up of cells of various sizes ranging from those just visible at the magnification of 40 diameters to the great Mauth-

ner's cells which are visible to the naked eye. The cells lie for the most part lateral and ventral to the fasciculi longitudinales medialis et lateralis, their dendrites extending to the periphery of the oblongata as is indicated on the left side of figure 4. The receptive field of the rostral end of the nucleus is, therefore, the whole area between the mid-line and the Vth and VIIth motor nuclei (figs. 3–4), while caudally it lies between mid-line and nucleus lateralis tegmenti (fig. 5). Golgi preparations show a dense neuropil in this region made up of the dendrites of the cells of the nucleus, collaterals from the primary sensory bulbar nuclei and from the long descending paths of the oblongata. The axones from the cells of the nucleus make up the greater part of the fasciculus longitudinalis medialis; the great majority of them descend in it, a few ascend, and some bifurcate into a large descending and small ascending ramus.

It is with the large cells that we are chiefly concerned. Their general relations and position in the cross section are indicated in figure 4 where they are seen to have large cell bodies and usually two dendrites, sometimes only one, directed ventro-laterally and branching in the neuropil near the periphery. The axone arises dorsally and turns into the fasciculus longitudinalis medialis. The Nissl substance (fig. 9) is in the form of discrete bodies, which, however, are not so large or regular in outline as they are in typical motor cells.

The other cells of the nucleus are either commissural or Golgi type II cells or belong to the short path (i.e., formatio reticularis) type. While the latter types form a continuous column, the large cells are arranged in groups which correspond to the distinct subdivisions of the nucleus found in larvae. At the level of these groups we find the dense neuropil and here the small cells are more numerous than elsewhere and extend farther laterally, so the groups are indicated in the reconstruction (fig. 2) by enlargements.

It will be seen in figure 2 that the nucleus is larger throughout the region of the primary VIIIth centers (*N.ac.vent.* and *N.ac.dors.*) and that its four rostral groups which are coextensive with the height of the secondary acoustico-lateral decussation show

the greatest specialization. According to my interpretation, certain cells of the nucleus in the acoustic region are differentiated from the rest of the nucleus to form part of a direct, highly medullated reflex path from the internal ear and lateral line organs to the motor nuclei of the swimming muscles; these are Mauthner's cell and the cells which I am homologizing with the Müller's cells of cyclostomes.

The nucleus may be roughly divided into three parts, which differ somewhat in their connections, though the differences are not sharply defined (figs. 1 and 2): (1) The rostral quarter, just referred to as the most highly differentiated portion, is related chiefly to the acoustico-lateral system and cerebellum and consists of four distinct cell groups. (2) An intermediate quarter (pars intermedia) extends through the greater part of the facial lobe and is related to the gustatory VIIth centers, as well as to the acoustic nuclei. (3) The caudal half (pars inferior) extends somewhat rostral and caudal of the vagal lobe, shows less specialization than the rest, and is least influenced by acoustic impulses but more so by impulses from the spinal Vth nucleus (fig. 2, *S.g.R.*) and the Xth nuclei.

Pars inferior. The caudal half of the nucleus motorius tegmenti is practically coextensive with the vagal lobe (fig. 2, *N.Mot.Teg.inf.*). It is less directly connected with the acoustico-lateral system than the rest, its cells are smaller, more diffusely arranged and in general less highly differentiated. It is very like the caudal part of the pars intermedia shown in figure 5. The connections of this part of the nucleus are mostly tactile and gustatory. The vagal connections have been described by C. J. Herrick ('05) and I can confirm his account for Ameiurus. The fibers from the nucleus intermedius vagi and the substantia gelatinosa Rolandi pass ventrally as internal arcuates and either cross in the ventral commissure or descend in the raphé to enter the nucleus motorius tegmenti of the opposite side. Some are uncrossed, as are the collaterals from the secondary visceral paths. Figure 2 shows the acoustico-lateral nuclei extending to the level of the pars inferior and impulses from these nuclei reach its rostral end. The efferent fibers of the group are difficult to

trace; most of them are delicate and doubtless go only a short distance rostrally or caudally. Some, however, can be seen entering the fasciculus longitudinalis medialis, here bifurcating and the stronger ramus ascending through the oblongata.

Pars intermedia. This division of the nucleus extends through the inferior part of the facial lobe, from which the secondary bundles pass ventrally into the secondary gustatory tract. Figure 2 shows it divided into two parts, the more caudal one has the same relation to the facial lobe as the inferior division has to the vagal lobe. Here too tactile impulses (from the substantia gelatinosa) reach it, together with the gustatory impulses. The relations with the external arcuates from the ventral acoustic nucleus are also well marked, as appears in figure 5. The superior part of the group is more intimately related to the acoustico-lateral system, numerous secondary fibers of which cross at this level; it has become in fact the dominant connection of the motor tegmental nucleus. The cells of the pars intermedia are larger and have more prominent ventro-lateral dendrites than are found at more caudal levels.

Just rostral to the pars intermedia (fig. 2), is a group of about six large cells whose dendritic field is identical with that of the small inferior VIth nucleus and both are reached by numerous fine fibers from the acoustic nuclei.

The four most rostral groups of cells extend through the height of the acoustico-lateral decussation and are most intimately associated with this system. There are more and larger cells and a denser neuropil in these groups than in any other part of the tegmental nucleus and the axones of the large cells are mostly descending.

The pre-mauthnerian and post-mauthnerian groups (*P.PreM.* and *P.Post M.*, fig. 2) are so closely related to Mauthner's cell that their dendritic fields are identical respectively with the superior and inferior ventral dendrites of that cell (p. 103). Their connections can best be taken up in connection with the discussion of Mauthner's cell (p. 104). In addition it should be noted that the posterior end of the post-mauthnerian nucleus has the same field as the large superior VIth nucleus. As is shown in figure 2,

the pre-mauthnerian group (*P.Pre M.*) is closer to Mauthner's cell, while the post-mauthnerian group (*P. Post M.*) is separated from it by a distinct interval. In some brains, in fact, the most caudal cells of the former group are found in the same transverse sections as the body of Mauthner's cell. The Müller cells of the post-mauthnerian groups are distinctive, but the other cells differ from those of more caudal levels only in that there are more and larger dendritic branchings in the ventro-lateral than in the ventro-medial field, as appears in figure 4. The cells of the pre-mauthnerian group are large, like those of the pars superior and pars suprema; it has about a dozen cells as large as the largest Müller cells of lower levels. Here too we find the densest neuropil ventro-laterally.

The two most rostral groups, pars superior and pars suprema, lie at the upper end of the acoustico-lateral decussation, with which they are intimately connected; and through the lemniscus lateralis they connect with all levels of the dorsal acoustic nucleus. At this level the fasciculus longitudinalis medialis and lemniscus are turning laterally and the cells of the nuclei of the motor tegmentum are also more lateral, so that most of them lie just ventral to the lemniscus. Like all other groups, they are closely related to both of these tracts. Both groups have another important connection: most of the fibers of the cerebello-tegmental tracts end in them. The direct cerebello-tegmental tract cannot be traced much farther caudally than the pars superior, and the pars suprema may be looked upon as the chief end-station of this system. The more caudal cerebellar system, which is relayed in what Tello has described as the preventricular tegmental nucleus, makes connections with the peri-mauthnerian groups, as well as with the pars superior. This system will be discussed at greater length in the paper on the acoustic nuclei. The pars superior is more intimately related to it than to the direct cerebellar path. The pars superior differs from the pars suprema also in that it, like the pre-mauthnerian group, is closely related to the nucleus princeps trigemini. Both of these groups have their dendritic fields farther laterally than the more caudal groups, and their dendrites extend somewhat rostrally as well; this con-

dition is doubtless correlated with the fact that the fasiculus longitudinalis lateralis (lemniscus) and the tecto-bulbar tracts are converging toward their end and origin respectively at these levels. Most of the cells of the pars superior are of the same size as those of the pars premauthnerea but six or seven are as large as the Müller cells of that group. Figures 8 and 9 show four cells of this group. There are, however, at the caudal end of the pars suprema nine or ten cells which, in the size of cell body and girth of dendrite surpass any other cells of the whole nucleus except the Mauthner cells themselves. They are as large as the Müller cells of this level (fig. 2) and are apparently homologous with Tello's 'nucleo motor tegmental anterior interno.' Every axone from this group descends in the dorsal part of the fasciculus longitudinalis medialis and constitutes the second link in the direct cerebello-spinal system. The tractus cerebello-tegmentalis-bulbi of Edinger ('08) and Franz ('11) and others does not extend throughout the bulbar tegmentum, so far as my observations go, but ends chiefly in the pars suprema and to a lesser extent in the pars superior nuclei motorii tegmenti.

To summarize the connections of the nucleus motorius tegmenti bulbi we may say:

1. The axones run in the fasciculus longitudinalis medialis, crossed and uncrossed, and most of them descend but some bifurcate into ascending and descending branches. A bundle of the largest accompanies Mauthner's fiber through the spinal cord.

2. The cell groupings are determined, in part at least, by the primitive relation to the somatic motor (III, IV, VI, spinal) and specialized visceral motor (V, VII, IX, X) nuclei, whose activities are coördinated by means of this nucleus and its tract, the fasciculus longitudinalis medialis.

3. All parts of the nucleus receive collaterals from the fasciculus longitudinalis medialis, the fasciculus longitudinalis lateralis and the tecto-bulbar system.

4. The caudal half receives collaterals from the tracts arising in the primary sensory nuclei of the Xth, VIIth and Vth nerves and to a lesser extent in the acoustico-lateral nuclei. The rostral half is very closely related to the acoustico-lateral system and to

the descending systems from the cerebellum. The fact that the nucleus discharges directly into the motor nuclei makes this sensory connection a short circuiting of the sensory path and is interpreted as an adaptation for rapid reflexes.

Müller's cells. These cells, which I am treating separately from the rest of the nucleus motorius tegmenti merely for the sake of clearness, differ from their fellows in three ways: they are larger, the cell body lies dorsal to the fasciculus longitudinalis lateralis just under the acoustic decussation and they are confined to the levels of the acoustico-lateral nuclei (figs. 2 and 4). Some of them have, in addition to the ventral dendrites, a short lateral dendrite. These cells are fairly constant in number and position with relation to the subdivisions of the motor tegmental nucleus; those near Mauthner's cell are perfectly constant. The left side of figure 4 shows a reconstruction of one of the Müller cells of the pars postmauthnerea and one of its companions appears on the right side. (There are three close together at this level.) It is clear from the figure that the receptive field of this cell is the same as that of the other cells of the group except that it is more intimately related to the decussating acoustico-lateral fibers, by means of the lateral dendrite. The distribution and relative size of the Müller's cells may be seen at a glance in figure 2 where they are indicated by solid dots on the right side. It is clear that those in the four rostral groups of the nucleus motorius tegmenti, where the VIIIth and lateral line roots and secondary fibers are most numerous, are the largest and in these only can the lateral dendrites be identified. The Müller cells are the largest of their group (figs. 8–9, where all of the cells are taken from the pars superior). The caudal end of the pars suprema is an exception (p. 96). Like other cells of the nucleus, their axones enter the fasciculus longitudinalis medialis, within which most of them descend, but some bifurcate into ascending and descending rami. These axones are the largest found in the oblongata, with the exception of the Mauthner's fibers. Some cross at once, as the Mauthner's fibers do, others descend a short distance before crossing, and still others give off crossed collaterals from time to time. Many, but not all, surround Mauthner's fiber in the bundle

which, caudal to Mauthner's cell, is separated from the rest of the fasciculus longitudinalis medialis by the internal arcuate decussation. Wallenberg ('07) has termed this bundle 'fasciculus octavo-motorius,' but the term is hardly justified, as it should include only the coarse fibers of this bundle, the fine ones having descended from the mesencephalic (and diencephalic?) tegmentum. Moreover, all the 'octavo-motorius' fibers are not included within it, and the axones of the Müller cells of the partes suprema et superior are as much concerned with the cerebello-bulbar and cerebello-spinal systems as with the octavus (p. 95).

The homologizing of these cells with the Müller cells of cyclostomes, as Edinger has done, possibly requires further evidence, though the observations of Johnston ('02), Edinger ('08) and others leave little room for doubt that in cyclostomes the cells which give rise to the Müllerian fibers are merely the largest elements of the nucleus motorius tegmenti. Their position between their tract, the fasciculus longitudinalis medialis, and the visceral motor nuclei is the same in all Ichthyopsida; more important are the facts that in the cyclostomes, ganoids and teleosts the bulbar cells are confined to the acoustico-lateral levels and most of the axones descend. Johnston ('02) counted from twenty to twenty-four giant fibers at the caudal end of the bulb in Petromyzon, although there were but seventeen or eighteen Müller cells in that region of the brain. The others presumably came from the mesencephalon. There are from twenty-five to twenty-seven bulbar Müller cells in Ameiurus and at the caudal end of the oblongata their axones *are* the giant fibers, since the mesencephalic fibers are reduced in caliber at this level. It should be said at this point that Johnston found an additional pair of cells larger than all the others just behind the motor VIIth roots. That these are homologous with Mauthner's cells there can be little doubt, as will appear below. The similarities in relations, receptive fields and internal structure between the ordinary cells of the motor tegmental nucleus, the Müller cells and the pair of Mauthner's cells will be discussed under the head of Mauthner's cell.

The one objection that can be raised to this interpretation, so far as I can see, is that in the cyclostomes the fibers from Müller's cells are uncrossed. This is not a matter of fundamental importance in view of the fact that the axones of the various nucleus motorius tegmenti cells (including the Müller cells) show every transition from immediate crossing to an uncrossed fiber which gives off crossed collaterals from time to time.

Edinger considers Deiter's nucleus an integral part of the nucleus motorius tegmenti. This matter will be taken up in my report upon the acoustico-lateral centers.

MAUTHNER'S CELL

Position, general relations and size. The position of Mauthner's cell is constant in its relation to the motor VIIth root and the cerebellum both in the larvae and adults of the teleosts studied. There is even little individual variation except in dorso-ventral position, i.e., it is farther from the ventricle and nearer the rest of the motor tegmental nucleus in some cases than in others. The cell body lies just rostral to the genu of the VIIth nerve and at the caudal end of the cerebellar peduncle. At this same level in all larval brains and in the adult Menidia, Salmo, etc., we find the anterior VIIIth root and the large-celled ventral acoustic nucleus (Deiters' nucleus), as may be seen in figure 6. In adult siluroids, however, the ventral VIIIth nuclei do not extend so far rostrally as Mauthner's cell (fig. 3). In so much as the principal connections of Mauthner's cells are with the VIIIth roots and nuclei there are certain significant differences between the cell and its synapses in Ameiurus and Salmo, as will appear below.

The primitive teleostean Mauthner's cell is not unlike a spindle bent to a right angle at the middle. The lateral limb is directed somewhat caudally, the ventral limb rostrally, so that a plane including both must be oblique to the brain axes. The axone (Mauthner's fiber) arises medially, from the apex of the angle, turns abruptly caudally and decussates with its fellow. It has long been known to extend throughout the spinal cord, giving

off collaterals to the motor nuclei. I have little to add to the excellent descriptions of Tagliani ('05) and Beccari ('07); I would say, however, that there is no evidence in my material of fusions such as Beccari describes between the collaterals of Mauthner's fiber and the dendrites of ventral horn cells. These collaterals are more obvious, and I am inclined to believe more abundant, in the young larvae than in older larvae and adults, as Tagliani says.

The great size of Mauthner's cell becomes apparent when in the reconstructions it is compared with the Müller's cells and the cells of the nucleus motorius tegmenti (figs. 3–5, and 7–9) or with the outlines of the large cells of Deiters' nucleus (fig. 6). It is always difficult to calculate the size of a multipolar cell, but an estimate will give a fairly concrete idea of the differences between Mauthner's cell and the other cells of the nucleus motorius tegmenti. Measuring from the sections of a young adult (fig. 7) the cell body (perikaryon) measured $66 \times 63 \times 60\ \mu$. If the dendrites be taken into account, the volume would be tripled. The dimensions of the Müller's cell shown in figure 8 are $63 \times 30 \times 26\ \mu$. The total volumes would be related as about seven to one, yet in this case the Mauthner's cell nucleus is but very little larger in actual size than that of the Müller's cell; the usual relation of the diameters is as one to one and a half. It is clear, then, that the nucleus of Mauthner's cell is small in comparison with the cytoplasm (see especially figs. 6, 10 and 11). The same holds true for the Müller's cells as may be seen at a glance in figures 8 and 9.

Dendrites. Certain dendrites of Mauthner's cell are constant in their position and connections. In the typical and simplest forms there are two gigantic dendrites and numerous small ones. This is the condition described by Mayser ('82) in Cyprinoids, Beccari ('07) in Salmo and Salamandrina, Tello ('09) in Salmo, Leuciscus and Cyprinus, C. J. Herrick ('14) in Amblystoma, and I have found it to be the case in all of the teleosts studied except Ameiurus. Figure 6, reconstructed from the brain of a 32 mm. trout larva, shows the lateral dendrite (*Lat.Dend.*) of authors and the ventral one, which will be called the superior ventral

dendrite (*S.Vent.Dend.*). The former extends almost to the lateral periphery of the oblongata branching among the VIIIth root fibers and the cells of Deiters' nucleus. The ventral one extends somewhat rostrally and branches widely in the neuropil formed by collaterals from the tracts of the ventro-lateral columns and by the dendrites of the pre-mauthnerean group of the nucleus motorius tegmenti (fig. 2). It is interesting to note that the girth of these large dendrites is relatively greater in larvae than in adults, as may be judged from figures 6 and 11. In addition to these two, Beccari describes in Salmo a medium-sized dendrite branching in the fasciculus longitudinalis medialis (*Med. Dend.* of fig. 6). This is almost always present and fairly constant in its relations. The small ventral dendrites related primarily to the fasciculus longitudinalis lateralis (Mayser '82) are more variable in number and position and are apparently more numerous, certainly more obvious, in the larva than in the adult. There is another type of dendrite, less conspicuous than the others, which has hitherto escaped notice. These arise from the region of the axone hillock; two of them are labelled *C.Dend.* in figure 11. It must be remembered that all of these dendrites do not lie in a single plane, but are so projected in figures 3, 6 and 11.

The dendrites will now be considered in more detail with especial reference to their appearance in Ameiurus.

Lateral dendrite. The lateral dendrite is theoretically the most significant, for it is almost exclusively related to the periphery, and this direct relation to the VIIIth root is the only fundamental character which distinguishes Mauthner's cell from the other cells of the nucleus motorius tegmenti. According to Beccari ('07) it has only terminal branches, but figure 6 shows other small ones in the trout; they may be seen in Ameiurus in figures 3 and 10. The terminal branching was well figured by Beccari and figure 6 shows that the branching is confined to the region of Deiters' nucleus. There is no evidence in any teleost of the large dorsal branch of the lateral dendrite which in urodeles ramifies in the dorsal acoustic nucleus (Beccari, '07, Herrick, '14). In other words, the impulses entering the lateral dendrite come

chiefly from the vestibular nerve and are largely equilibratory in nature. According to Beccari, the root fibers which are related to the lateral dendrite in Salmo come from the ramus sacculi of the vestibularis. The evidence in Ameiurus is perfectly clear that fibers from both vestibular roots enter the bundle which surrounds the lateral dendrite. In view of Parker's ('09) work, on hearing in fishes they are not necessarily all equilibratory (p. 114).

The lateral dendrite retains its larval proportions more nearly than any of the others; the whole lateral side of the perikaryon tapers off into it. The series from which figure 10 is taken was cut in the plane of the lateral dendrite and so it appears without the foreshortening that comes of reconstructing a transverse series (figs. 6 and 11). Figure 10 shows that one, occasionally two, branches arise from it proximally, but these are slender and difficult to recognize.

The synapse between the lateral dendrite and the VIIIth root fibers in Salmo is as Beccari has described it, a simple neuropil in the midst of Deiters' nucleus. But the withdrawal of the VIIIth root from Mauthner's cell has brought about a change in siluroids which is manifested in all developmental stages. We may assume that in the course of phylogeny the VIIIth roots were crowded farther and farther back by the gustatory VIIth root, yet Mauthner's cell remained stationary and its lateral dendrite did not elongate. So at least we interpret the facts, which are as follows.

In the youngest Ameiurus larvae which I have studied (11 mm. long) and in all subsequent stages, the lateral dendrite does not arborize at the lateral periphery of the medulla as in Salmo, but ends farther medialward dorsal to the spinal V tract, and its terminal branches are reduced almost to nothing. This condition is shown in figure 3. The nature of the synapse is also altered from what it is in the more generalized fishes. The dendrite is enveloped in a sheaf of thick VIIIth root fibers which end in club-like expansions upon its surface (*unXed. VIII*, figs. 10, 11 and 13). The reduced terminal branching is shown in figure 10 at *Br.L.Dend.;* there are never more than two or three of these slender processes and they come into relation with col-

laterals of VIIIth fibers. The club-endings are the important part of the synapse and they constitute an unique feature of the siluroid brain. As the root fibers retain their thick myelin sheaths almost to the very end, the whole apparatus appears striking in transverse and horizontal series of hematoxylin, Weigert and Cajal preparations.

Since the elements of the synapse are very large, it is an exceptionally favorable material for the study of the nature of the synapse. The results of my study are embodied in figure 13, which was drawn from an adult brain fixed in formol-osmic-Zenker. In this and in all of the other brains fixed in strong osmic acid mixtures the plasma membranes around the club-endings of the VIIIth root fibers stand out very clearly. The same may be said of the limiting membrane of the lateral dendrite where it is cut squarely. In other words, there is no evidence of fusions between root fibers and dendrite; the two are merely in contact. The few insignificant branches of the lateral dendrite which might be interpreted as root fibers fused to the dendrite are readily distinguished from them by the facts that they taper down rapidly peripherally and have no myelin sheaths.

The ventral dendrites. In most teleosts there is but a single large ventral dendrite, as is shown in figure 6 for the trout larva (*S.Vent.Dend.*). Here it is as mighty as the lateral dendrite, it extends rostrally as well as ventrally and is profusely branched in the neuropil at the periphery of the oblongata. In Ameiurus the largest and most medial of the ventral dendrites (the superior ventral dendrite) has the same direction and position, as appears in figure 3. In this fish, however, there is always another ventral dendrite (inferior ventral dendrite) which reaches the ventral-lateral periphery. It is never so large or so profusely branched as the superior dendrite (fig. 11, *Inf.Vent.Dend.*); it arises laterally from the cell body and is directed caudally as well as ventrally (see fig. 3, left Mauthner's cell). In the cell reconstructed in figure 11 there were two such dendrites which is not a rare condition.

The two great ventral dendrites have certain distinct connections as well as different relations to the cell body. It has been

said (p. 94) that the superior ventral dendrite branches in the dendritic field of the pars premauthnerea nuclei motorii tegmenti and the inferior dendrite has the same relation to the pars post-mauthnerea. Accordingly what is said of these ventral dendrites holds also for the associated groups of the tegmental nucleus. The superior dendrite is characterized by its close relation to the nucleus princeps V. At no other level are the fine fibers which stream ventrally into the ventro-lateral neuropil of the same side so abundant as in the region of the pars premauthnerea, especially its caudal end where the superior dendrite ramifies. The fibers of the indirect cerebello-tegmental system can also be traced into this region but not farther caudally (p. 95). Moreover, it is obvious from what has been said of the position of the ventral acoustic nuclei in Ameiurus that in this form the superior dendrite is rostral to any part of these nuclei and it has no obvious connection with them as it has in Salmo. The inferior ventral dendrite, on the other hand, and its associated group (pars post-mauthnerea) are intimately related to the ventral acoustic nuclei. I would suggest the following as a reason for the phylogenetic development of the inferior ventral dendrite of Ameiurus: when in the hypertrophy of the gustatory system the ventral acoustic nuclei were crowded caudally and so separated from Mauthner's cell, the superior ventral dendrite retained its position because of its intimate relation to the chief Vth nucleus and cerebellum, while the inferior dendrite was developed to receive the impulses from the ventral VIIIth nuclei. The ventro-lateral neuropil is more dense in the region where these two dendrites and their associated cells branch than at any other level. That is because the collaterals from the long tracts, namely the tecto-bulbar system, the fasciculi longitudinales medialis et lateralis and from the acoustico-lateral decussation which reach all other parts of the nucleus motorius tegmenti are most abundant at this level. The chief impulses, then, which reach Mauthner's cell by way of its ventral dendrites come from the ventral acoustic nucleus, from the chief Vth nucleus, from the tectum through the crossed and uncrossed tecto-bulbar tracts and from the cerebellum by way of the indirect cerebello-tegmental system.

In addition to the long dendrites, there are small processes arising ventrally from Mauthner's cell and arborizing through and about the fasciculus longitudinalis lateralis. In one adult brain there were five of these but in most cases I have not found more than three. This is in marked contrast to the wealth of dendrites in the corresponding region of the cell in Salmo, as may be seen by comparing figures 3 and 11 with figure 6.

The minute dendrites which arise from the region of the axone hillock are described in the following section.

The axone cap. The structure which I am calling the axone cap has long been known, but its nature has not been analyzed hitherto. In this case, as in several others, Mayser ('82) came nearer the truth than anyone else since his day. On the basis of preparations of carp brains stained with carmine and with osmic acid, he concluded that this 'Klumpen' consisted of processes of nerve fibers and of ependymal fibers. Beccari ('07), working mainly with Cajal preparations, suggested that it might be a highly characteristic beginning of the myelin sheath of the axone, which as is well known, is very large. This is not the case, as may be seen in figure 11, where the sheath (*Md.Sh.*) of Mauthner's fiber is shown tapering down gradually toward the cap, and so far as my observations go, terminating before reaching it. Beccari did see some fibers which seemed to come from the neighborhood of the fasciculus longitudinalis medialis and apparently entered the 'massa,' or 'cap' as I suggest calling it.

In toluidin blue and erythrosin preparations the axone cap is most conspicuous, staining intensely red. In this sublimate fixed material it appears under high powers as a very dense neuropil, more dense even than the molecular layer of the cerebellum. It fits like a cap over the region of the axone hillock and the adjoining medial surface of the cell, the axone passes straight through the middle of it, as may be seen in figure 6 taken from a trout larva and figure 11 from a young Ameiurus. As has been said, Mauthner's cell is turned so that the lateral parts are caudal to the medial parts and the axone arises from the superior medial surface. This is, accordingly, the part of the cell body covered by the cap, which extends over the root of the superior ventral den-

drite. It never reaches the lateral dendrite, which seems to be connected only with VIIIth root fibers.

The axone cap is as striking and characteristic of Mauthner's cell as are its great size and remarkable connections. This study was undertaken primarily to analyze the cap, a point which was essential to a full understanding of the central connections of the VIIIth nerve. Although it is improbable that I have made out all of its component parts, its essential nature at least is clear. It is, in fact, a peculiar synapse such as has not been found, so far as I know, in any other nerve cell. It is made up of at least three kinds of fibers, two of them nervous, the other supporting. These are: (A) collaterals from various neighboring fibers; (B) minute dendrites from the underlying region of the cell body; (C) supporting elements.

A. The collaterals ending in the axone cap stand out most clearly in Cajal preparations and are clearer in the older larvae than in the younger. Since Beccari ('07) worked mainly on young larvae, this accounts doubtless for his uncertainty concerning the nature of the axone cap in Salmo, where in reality it is essentially the same as in Ameiurus described below. The feltwork of collaterals is best shown in figure 10, in which the detail of the cap was drawn from a single 8 μ section. Even though the cell body had shrunken away from the cap, the relations of the fibers are perfectly clear. The figure shows three kinds of fibers giving off collaterals. First, there are thick fibers, most of which are from the VIIIth root. Those which have already crossed the mid-line are cut longitudinally (*Xed.VIII*); the uncrossed VIIIth root fibers are cut transversely. The latter form a fascicle of very thick fibers and are characteristic of Ameiurus. They ascend from the root of the same side and at the level of Mauthner's cell turn rostrally, giving off collaterals to the cap through its entire extent. As the figure shows, there are two kinds of terminations in the cap, the fine free endings and the knob endings (*K.End.*), the latter in contact with the surface of the cell. This point is evident in figures 11 and 12, which are taken from a brain fixed in formol-osmic-Zenker, a fixation which produces less distortion and shrinkage in this material than any

other I have found. We may safely assume that the form relations in this preparation are more nearly true to life than they are in Cajal preparations; a comparison of the collaterals arising from the large VIIIth fibers of the axone cap in figures 10 and 12 is particularly illuminating in this connection. It need hardly be said, however, that the details shown in figure 12 could hardly be interpreted if one had not first studied the more obvious pictures given by Cajal preparations. Besides the collaterals from the VIIIth root fibers, numerous collaterals are given off from the secondary VIIIth fibers (fig. 10) as they stream past Mauthner's cell before crossing the mid-line to ascend as the acoustic lemniscus.

Fibers from the fasciculus longitudinalis medialis are almost as numerous as those from the VIIIth roots. They seem for the most part uncrossed and are gathered into two bundles. One of these consists of fine fibers from the infracommissural bundle of the tract which enter the axone cap ventro-medially. A few of them are shown in figure 10 (*Col.F.L.M.*), where their small size as compared with the VIIIth roots fibers is apparent. They stand out clearly in hematoxylin preparations as a loose bundle of unmedullated fibers and are doubtless collaterals from descending fibers. The other bundle of fibers is unique; it has not been recognized hitherto in fishes, but C. J. Herrick ('14) has described it in Amblystoma and I have found indubitable evidence for it only in osmic acid preparations. It is a bundle of small medullated fibers which can be traced with a fair degree of certainty from the mesencephalic nucleus of the fasciculus longitudinalis medialis. It leaves the supracommissural bundle of the homolateral tract, where Mauthner's fiber swings around it (figs. 3 and 6), and envelops the fiber to the point where it emerges from the axone cap. Here its fibers lose their sheaths and ramify as free endings in the cap.

Most of the endings in this extraordinary synapse may be grouped in one of three classes: fibers from the fasciculus longitudinalis medialis, collaterals from the secondary acoustico-lateral tract and, most important, collaterals of VIIIth root fibers from the same and the opposite side. The predominence of the

last type of fiber gives reason to believe that the axone cap has developed pari passu with the great lateral dendrite and both are expressions of the intimate relation of this nucleus motorius tegmenti cell with the VIIIth nerve; hence Mauthner's cell is the only one which has them.

B. The cap dendrites. In figure 10 certain processes are shown extending from the body of Mauthner's cell across the shrinkage space in this region toward the axone cap. They can be recognized in most good Cajal preparations but judging from them alone they might well be considered artefacts. In formol-Zenker material the picture is clearer (figs. 6–7) and after formol-osmic-Zenker fixation their true nature can be best appreciated. Thus, in figures 11 and 12 they are seen to be delicate dendrites extending through or ramifying in the cap. There may be as many as eight of them, but for the sake of clearness most are omitted from figure 11, which represents a drawing of several superimposed sections. These dendrites obviously increase the receptive field in the region of the axone cap and they receive impulses from the felted collaterals, whereas the knob endings (figs. 10 and 12, *K.End.*) transmit impulses directly to the cell body.

C. Supporting elements. There is no evidence that, as Mayser supposed, ependymal fibers enter the axone cap but there *are* supporting elements in it. In figure 11 scattered cells are shown at the surface of the cap (*Gl.a.*) and a similar cell (*Gl.b.*) nearby sends out two delicate fibers toward it. These cells are more clearly seen at a higher magnification in figure 12; here they appear as stellate elements sending processes into the cap and the surrounding neuropil (cf. *Gl.c.*). I have interpreted them as neuroglia cells for the following reasons:

1. They show no evidence of Nissl substance even in the adult, where the cytoplasm is frequently well preserved.

2. Preparations which show excellent preservation of all nerve cells have some of these cells very poorly fixed. Huber mentions this as a feature of the glia cells of the frog and it appears in figure 11.

3. The cells anastomose with one another, as may be seen in the case of the cell *Gl.b.* and its neighbor in figure 12. We find

such appearances in the vertebrate central nervous system only in glial elements.

4. The nucleus frequently shows two chromatin nucleoli and in many cells there are evidences of amitosis (e.g., *Gl.a.*, *Gl.b.*, *Gl.c.*, *Gl.d.* of figure 12).

5. The structures shown at *Gl.b.* in figure 11 were abundant in this preparation and were interpreted as neuroglia fibers. Some experiments with specific neuroglia stains were not successful, however.

The pericellular net or basket ('canestro'), of Mauthner's cell forms a thick dense sheath for cell body, dendrites and axone. It has been admirably described and figured by Beccari ('07) and I have nothing further to add except certain additional types of fibers which are included in the following summary.

Mauthner's cell is, as Beccari and Tello have pointed out, a nucleus in itself, for the associated groups of the nucleus motorius tegmenti have not all the connections which it has. We can determine definitely how many different kinds of impulses may reach a single nerve cell in this case, and as the sequel shows the number is surprising.

1. Vestibular root fibers: (a) Homolateral fibers ending upon the lateral dendrite. (b) Homolateral fibers giving off collaterals to the axone cap. (c) Contralateral fibers giving off collaterals to the axone cap and pericellular net.

2. External and internal arcuate fibers from the ventral acoustic nucleus to the pericellular net of the inferior ventral dendrite.

3. Axones and collaterals from the dorsal acoustico-lateral nucleus: (a) Collateral endings in the axone cap from decussating fibers crossed and uncrossed. (b) Endings of collaterals and axones in the pericellular net. (c) Collaterals from lower levels of the dorsal nuclei via the fasciculus longitudinalis lateralis to the pericellular net.

4. Fibers from the fasciculus longitudinalis medialis: (a) Endings in the axone cap from the mesencephalon. (b) Collaterals from the ventral bundles of the tract to the pericellular net and the axone cap, mostly uncrossed.

5. Cerebello-tegmental fibers, for the most part to the pericellular net of the superior ventral dendrite.

6. Collaterals from the crossed and uncrossed tecto-bulbar tracts to both ventral dendrites.

7. Fibers from the nucleus princeps trigemini to the pericellular net of the superior ventral dendrite.

It is obvious that the chief connections of Mauthner's cell are with the vestibular nerve and its nuclei; most of the other fibers come from the acoustico-lateral nuclei, the fasciculus longitudinalis medialis and the tecto-bulbar system. These fibers and all others here described bring data concerning the orientation of the animal in space. It should also be noted that the lateral, superior ventral and inferior ventral dendrites each have certain distinctive fiber connections.

The internal structure of Mauthner's cell. Certain cytoplasmic characters of this giant cell stand out clearly in ordinary histological preparations (i.e., iron hematoxylin after formol-Zenker fixation), and the following incomplete description is given in the hope that it may serve as a basis for further work. The account is incomplete because time was wanting to make the necessary experiments in technique and there is little doubt but that all of the typical cytoplasmic elements described by Cowdry ('12) could be studied during various physiological activities. This applies to the Müller cells as well as to Mauthner's cell, for in both cases cells having the same functional connections, in fact, identical cells of different individuals could be studied under varying conditions. Attention is called to figure 7 in this connection, for in this brain only Mauthner's cell and certain of the Müller's cells showed cytological signs of fatigue.

Nissl bodies. The chromidial substance is distributed evenly through the cell body and bases of the dendrites and is in the form of flakes arranged in rows more or less parallel to the surface. It appears thus after all the fixations which I have used, viz., formol- and formol-osmic-Zenker, Orth's fluid, strong Flemming, and Bensley's acetic-osmic-bichromate mixture. The Nissl bodies are relatively small as compared with those of motor cells, very numerous (Tagliani to the contrary notwithstanding), irreg-

ular and elongate, as may be seen in figures 6, 11 and 12. Figures 7, 8 and 9 show that the Nissl bodies of the Mauthner's cells, the Müller's cells and the other large cells of the nucleus motorius tegmenti are practically identical in size and shape, though they are not so abundant in the last mentioned type. They are, in fact, quite distinctive of the cells of this nucleus.

Neurofibrillae. All kinds of preparations show neurofibrils in Mauthner's cell, provided only the sections are cut thin enough. Mayser saw them clearly in his carmine preparations. This is, in fact, an ideal material for studying the chromidial substance and fibrillae side-by-side under different physiological conditions of fatigue, etc. It is interesting to note that in many Cajal preparations the fibrillae appear thicker in Mauthner's cell than in any others, but this difference cannot be perceived in the more reliable formol-osmic-Zenker material.

The mitochondria and other cytoplasmic granulations have not been studied carefully because they are not sufficiently well preserved in my material to make the identification certain. The great medullary sheaths on the periphery of the oblongata reduce the osmic acid rapidly so that it does not penetrate in time to fix these structures. In Mauthner's fiber the mitochondria are short rods arranged parallel to the neurofibrillae. Similar structures are shown in figure 13 within the lateral dendrite, but they cannot be definitely identified as mitochondria. The granules shown in figure 12 doubtless correspond to Held's neurosomes, but as Cowdry ('12) has shown this term includes two distinct categories of cytoplasmic granulations which are not distinguishable after sublimate fixation.

DISCUSSION

The nucleus motorius tegmenti bulbi is primitively a coördinating mechanism for the motor apparatus of the bulb and cord. Edinger has emphasized the importance of this point and it is substantiated by the position of the nucleus in the somatic motor column, by its relation to the fasciculus longitudinalis medialis, by the internal structure of the cells and their grouping in the region of the bulbar motor nuclei. The last point has not been

recognized hitherto, for it is not clear except in larval brains. In all fishes certain cells of the nucleus have enlarged and otherwise differentiated as a result of direct connections with the primary sensory centers of the bulb. This connection has short-circuited the primitive reflex path between the sensory centers and the motor nuclei of bulb and cord. The sensory connections of the nucleus have been emphasized by Cajal and others. The most important path so developed was between the acoustico-lateral centers and the motor nuclei of the muscles used in swimming. In the region of the acoustic centers we find highly differentiated cells of the nucleus motorius tegmenti arranged in pairs on either side of the mid-line, close under the acoustico-lateral decussation, whither they have presumably migrated in response to the close association with the acoustic system (Kapper's neurobiotaxis). These great cells are probably homologous with the Müller's cells of cyclostomes and they agree with them further in that the axone does not usually cross at the level of the cell body.

One pair of such cells has established a direct connection with the vestibular root fibers by means of an enormous lateral dendrite and a peculiar synapse termed the axone cap. They are the cells of Mauthner and are among the largest and most highly differentiated nerve cells we know. This view of the origin of Mauthner's cell is based upon the following facts. In the cyclostomes there is a pair of enlarged Müller cells at the anterior VIIIth level in exactly the same position as the teleostean Mauthner's cells, differing from the latter chiefly in that the axones are uncrossed. In as much as we find in the teleostean Müller cells all transitions from an uncrossed to a crossed condition (p. 99), this is not a particularly significant difference. The Müller cells of Ameiurus show transitions from the large cells of the nucleus motorius tegmenti to the Mauthner cells in other respects such as internal structure. Furthermore, Mauthner's cell receives all of the impulses which are common to every part of the nucleus since its ventral dendritic field is identical with that of the associated groups of the nucleus. Finally, the axone of Mauthner's

cell runs in the tract of the nucleus motorius tegmenti, namely the fasciculus longitudinalis medialis, in company with the Müller's fibers, and connects up with the same classes of motor cells.

Mauthner's cell differs from the other cells of the nucleus in its direct, intimate connection with the periphery. It has carried the short-circuiting one step farther than the Müller cells, so that it is part of a three-neurone reflex consisting of an acoustic ganglion cell, Mauthner's cell, and a motor cell of the ventral horn. The reduction of the latent period by the elimination of the synapses and the highly medullated character of the system have led me to believe that we are dealing here with a reflex in which speed and precision are very important, and I would suggest that it is this reflex which enables the animal to keep perfect control of its equilibrium in the most rapid and intricate movements. We find the system most highly developed in the teleosts, whose tail swimming is ne plus ultra. If, as Edinger and others have taught, Mauthner's cell were part of the general tonus reflex, it is hard to see why it should have been so intimately related to the tail-muscle nuclei as to disappear as soon as the tail is lost in the anuran Amphibia. There are other reasons for believing that Mauthner's cell serves to keep the animal in equilibrium by means of tail and fin movements, rather than that it distributes tonus impulses generally to the somatic musculature. In the first place, it connects only with motor nuclei caudal to the motor VIIth root and in the adult the collaterals of Mauthner's fiber seem to be chiefly related to the fin and tail nuclei (Tagliani '05). Secondly, the great caliber of the axones, the broad contact surfaces in the synapse of the lateral dendrite, the highly insulated character of the whole path and the short-circuiting just referred to, all point to a very rapid reflex. Thirdly it must be remembered that Mauthner's cell has connections, not only with the VIIIth nerve, but from every center in the brain which receives impulses that may be used in equilibration (p. 109).

It is by no means necessary, however, that Mauthner's cell be concerned only in equilibratory reflexes. It has been said that

most of the root fibers which end about Mauthner's cell are thick fibers. Mullenix ('09) has found that some 'giant' fibers end in every crista and macula of the internal ear and I would interpret such fibers as paths of relatively low resistance, i.e., the fibers concerned in the most rapid reflexes. Now according to Beccari ('07), the lateral dendrite is related exclusively to saccular fibers in Salmo and in Ameiurus certainly some fibers from the macula sacculi end upon the lateral dendrite. It may well be then that Mauthner's cell is concerned in the characteristic auditory reflex in teleosts described by Parker ('08). This is a "sudden jump forward" after strong auditory stimulation. The course of such a reflex might be outlined thus: from the giant fiber endings in the macula sacculi, which latter Parker has shown to be sensitive to auditory stimuli, via the ganglion and posterior VIIIth root to the lateral dendrite; thence by way of Mauthner's fiber to the motor nuclei of the tail muscles.

The two characteristic synapses of Mauthner's cell in Ameiurus are noteworthy because they afford a valuable material for the study of the morphology of the synapse. My material has been fixed by methods which are recognized by cytologists who control their work by the study of living cells, as producing a minimum of artefact. The study of this material with a 1.5 mm. apochromatic immersion lens reveals no indications of a fusion of fibers, either in the very dense neuropil of the axone cap or in the enormous synapse between the VIIIth root fibers and the lateral dendrite. In the formol-osmic-Zenker and acetic-osmic-bichromate (Bensley) preparations of the latter synapse, there is a distinct plasma membrane over the root fibers and where the lateral dendrite is cut squarely a similar membrane can be distinguished around it (fig. 13). If my interpretation of the facts be accepted, this synapse is one where there is very little delay, and yet we find two synaptic membranes. The need of control of the fixation in cases where there seems to be a fusion of nerve processes of different neurones cannot be too greatly emphasized. Methods which involve the deposition of metallic salts give pictures which cannot be implicitly relied upon, especially in the central nervous system where the penetration of

fixatives is very slow. Beccari ('07) observed a fusion of collaterals from Mauthner's fiber with ventral horn cells in Cajal preparations fixed in alkaline alcohol but the well fixed material studied by Tagliani ('05) and my own sections show only a contact in these synapses.

SUMMARY

The nucleus motorius tegmenti may be divided into cell groups which correspond to the various motor nuclei of the medulla oblongata and the relations with these nuclei represent the primitive connections of the groups.

The groups have secondarily acquired relations with the primary sensory nuclei which lie at the same transverse levels and have differentiated accordingly.

This connection is interpreted as an adaptation for rapid reflexes between the sensory centers and motor centers of the somatic musculature.

The axones of the larger cells of the nucleus motorius tegmenti comprise the greater part of that portion of the fasicculus longitudinalis medialis which goes to the spinal cord.

The motor tegmental nucleus is best developed in the region of the acoustico-lateral nuclei.

Certain cells here have migrated toward the acoustico-lateral decussation, from which they receive collateral fibers, and they have increased in size. They are homologized with the Müller's cells of cyclostomes.

Mauthner's cell is interpreted as a cell of the same type as the Müller's cells which has gone much further in its differentiation as a result of establishing a direct connection with the VIIIth root fibers (p. 112). It is the association cell of three-neurone reflexes having short latent periods. The perikaryon and dendrites are gigantic in their proportions but the nucleus is not correspondingly large.

At least twelve different types of fibers have endings in the pericellular net of Mauthner's cell (see summary on page 109). One portion of the pericellular net is particularly highly devel-

oped. It is termed the axone cap and is primarily an acoustico-lateral connection.

There is clear evidence that the different dendrites of Mauthner's cell have different types of connections. The endings of the VIIIth root fibers upon the lateral dendrite in Ameiurus are well adapted for a study of the nature of the synapse. The two plasma membranes are seen in contact. The cell affords an excellent material for the study of the structure of the cytoplasm.

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REFERENCE LETTERS

Ac. Com., acoustico-lateral decussation
Ant. VIII, anterior root of nervus acusticus
Ax., axone
Ax. Cp., axone cap
Ax. Hill, axone hillock
Cap., capillary
CBL., cerebellum
Cbl. Cr., cerebellar crest
C. Dend., axone cap dendrite branching in the cap
Col. F.L.M., collateral from fasiculus longitudinalis medialis
F.L.L., fasciculus longitudinalis lateralis
F.L.M., fasciculus longitudinalis medialis
F.tect.bulb., fasiculus tecto-bulbaris
Gla, Glb, Glc, Gld, glia cells
Gust.VII, gustatory component of VIIth nerve
K.End., knob ending
L.Dend., lateral dendrite
Lat.Dend., lateral dendrite
Leuc., leucocyte
L.L.VII, lateral line component of VIIth nerve
L.L.X. lateral line component of vagus
Lob.VII, lobus facialis
Lob.X., lobus vagi
M.C., Mauthner's cell
Md.Sh., myelin sheath
Med.Dend., medial dendrite
M.F., Mauthner's fiber
Mot.V., nucleus motorius trigemini
Mot.VII, nucleus motorius facialis
Mül.C., Müller's cell
M.VII, ramus motorius nervi facialis
M.IX, ramus motorius nervi glossopharyngei
N.ac.dors., nucleus acustico-lateralis dorsalis
N.ac.vent., nucleus acusticus ventralis
N.amb., nucleus ambiguus
N.cerv.I, nucleus motorius nervi cervicalis I
N.Mot.Tegm., nucleus motorius tegmenti
N.lat.tegm., nucleus lateralis tegmenti
N.Mot.Teg.Inf., nucleus motorius tegmenti pars inferior
N.Mot.V, nucleus motorius trigemini
N.pr.V, nucleus princeps trigemini
Nucl.D., nucleus acusticus ventralis Deitersi
N.VI, nucleus nervis abducentis
ol., oliva inferior
Pc.Net., pericellular net
P.Int., pars intermedia nuclei motorii tegmenti
P.Med., periphery of medulla oblongata
P.PostM., pars postmauthnerea nuclei motorii tegmenti
P.PreM., pars premauthnerea nuclei motorii tegmenti
P.Sup., pars superior nuclei motorii tegmenti
P.Supa., pars suprema nuclei motorii tegmenti
S.g.R., substantia gelatinosa Rolandi
Sp.V, radix spinalis nervi trigemini
Sup.Vent.Dend., superior ventral dendrite
S.Vent.Dend., superior ventral dendrite
S.IX, ramus sensitivus nervi glossopharyngei
Un.Xed VIII, uncrossed eighth root fiber
Xed VIII, crossed eighth root fiber
V.Ac.Dec., ventral acoustic decussation
Vent.IV, ventriculus quartus
V.F., floor of fourth ventricle
2° Gust., secondary gustatory tract
2° VII, secondary gustatory bundles from lobus facialis
2° VIII, secondary eighth fibers
V+VII, facialis et trigeminis nervi
VIII, eighth nerve or root fiber of eighth nerve
X, nervus vagus

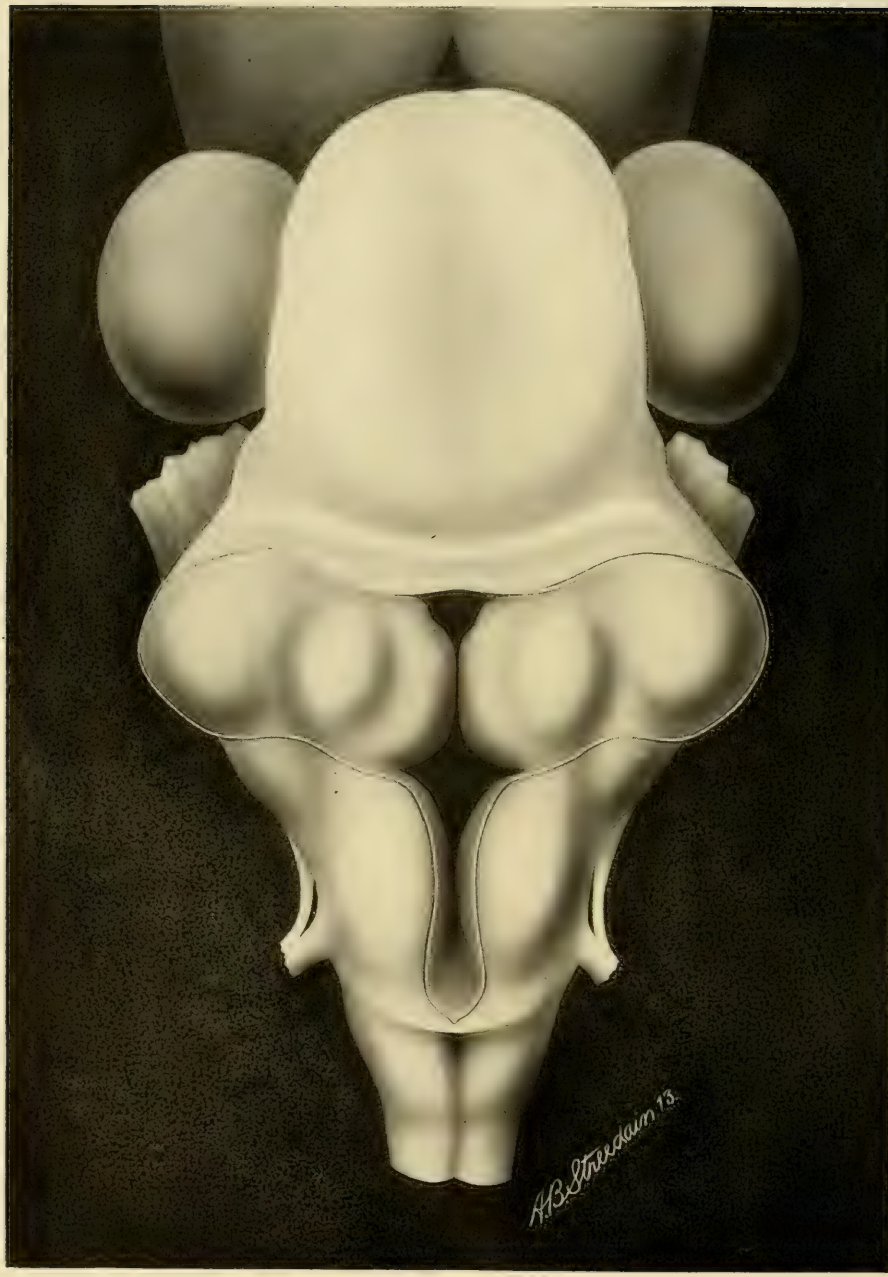


Figure 1

In all the drawings of sections the vertical arrow points dorsally, the horizontal one laterally. Figures 1, 2, 7, 8 and 9 were drawn by Mr. A. B. Streedain, who also helped me with all of the other illustrations.

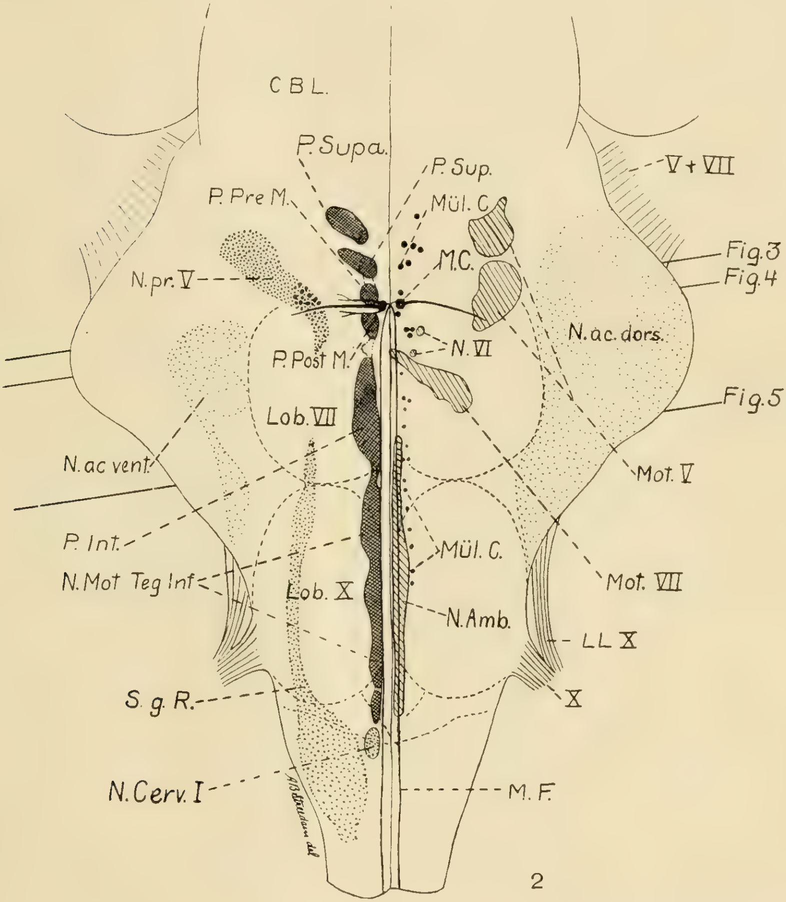
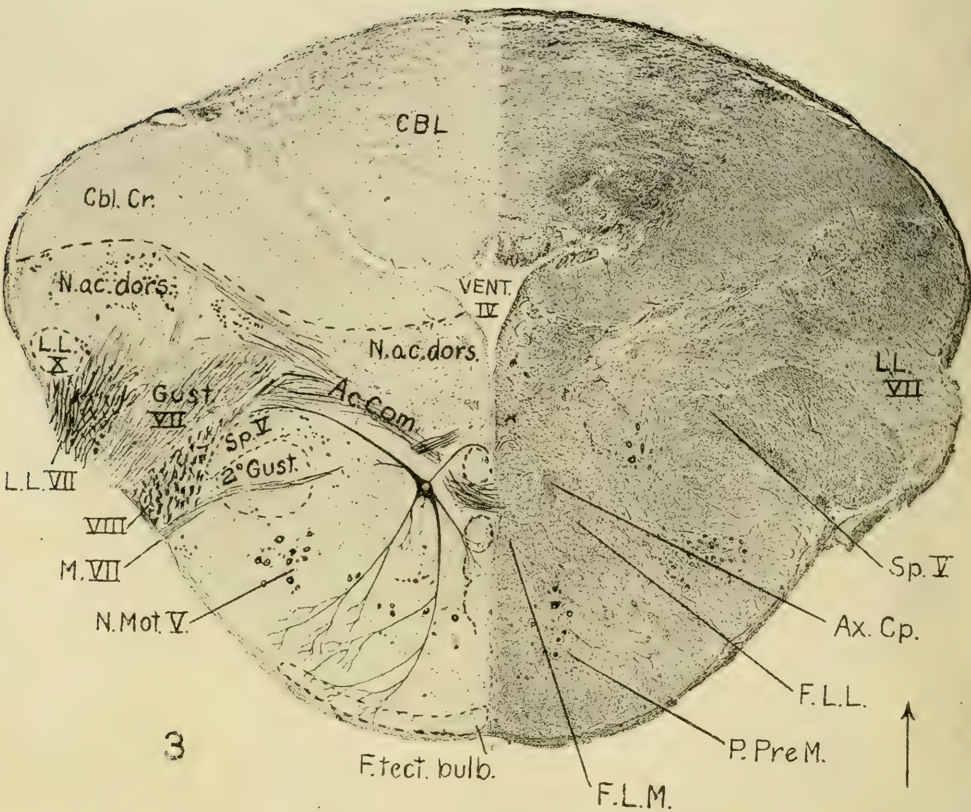


Fig. 1 A dorsal view of the cerebellum and medulla oblongata of a young Ameiurus melas fixed in formol. Drawn under a Zeiss binocular and magnified 15 times; for key see figure 2.

Fig. 2 A projection of the nuclei of the medulla oblongata of Ameiurus upon the horizontal plane. The cell groups are drawn in on the outline of figure 1, and are based upon projection reconstructions of a young adult Ameiurus melas 12 cm. long. The facial and vagal lobes are outlined by broken lines; Mauthner's cell and the Müller's cells are in solid black on the right side; the nucleus motorius tegmenti is indicated by double cross-hatching on the left side; the acoustic nuclei are in fine dots, only the lateral parts of the dorsal acoustic nucleus being shown; the sensory trigeminal nucleus in coarse dots; the visceral motor nuclei (of nerves IX, X, VII and V) are shown by single cross-hatching.



Figs. 3–5 Three photographs from a transverse series of the brain of a young adult Ameiurus melas 83 mm. long, stained with toluidin blue and erythrosin; magnified 38.2 diameters. The right side is the untouched photograph, the left is printed lightly and certain details drawn in with ink. The levels of the sections are indicated in figure 2.

Fig. 3 A section taken through the caudal end of the cerebellum including the axone and axone cap of Mauthner's cell on the right side and the middle of the left cell (which is projected entire upon this level). The dendrites in this case could be traced through 13 of the 10 μ sections as the series was cut oblique to the plane in which they lie. The more lateral of the ventral dendrites is the inferior ventral dendrite, the more medial, the superior ventral dendrite.

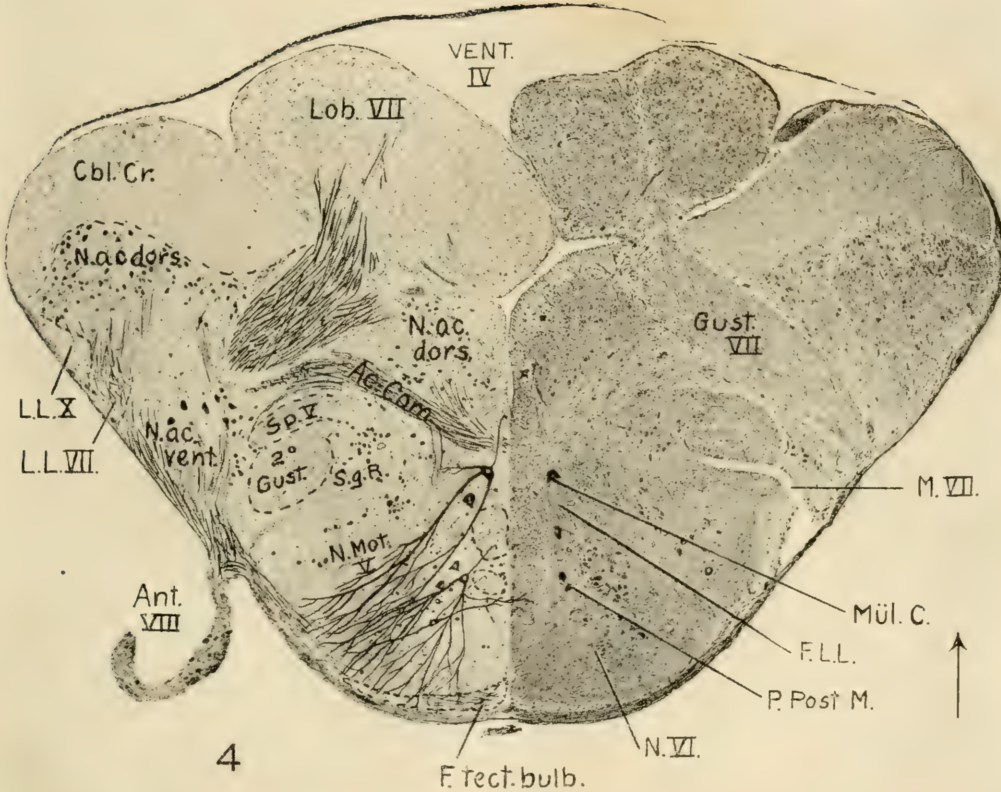


Fig. 4 A section taken at the rostral end of the lobi faciales, including a Müller's cell on either side. The cells on the left are drawn in on the basis of Cajal and Golgi preparations, to indicate the dendritic field of the nucleus motorius tegmenti.

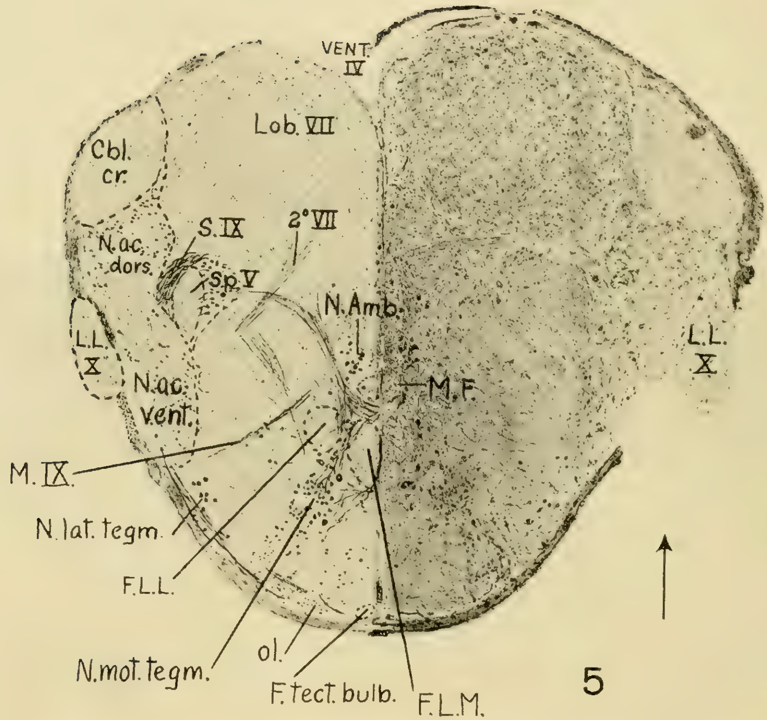


Fig. 5 A section taken through the caudal end of the lobi faciales at the level of entrance of the lateral line Xth root. The relations of the internal and external arcuate fibers and the position of the nucleus motorius tegmenti are shown, and especially the relation of the latter to the internal and external arcuate fibers.

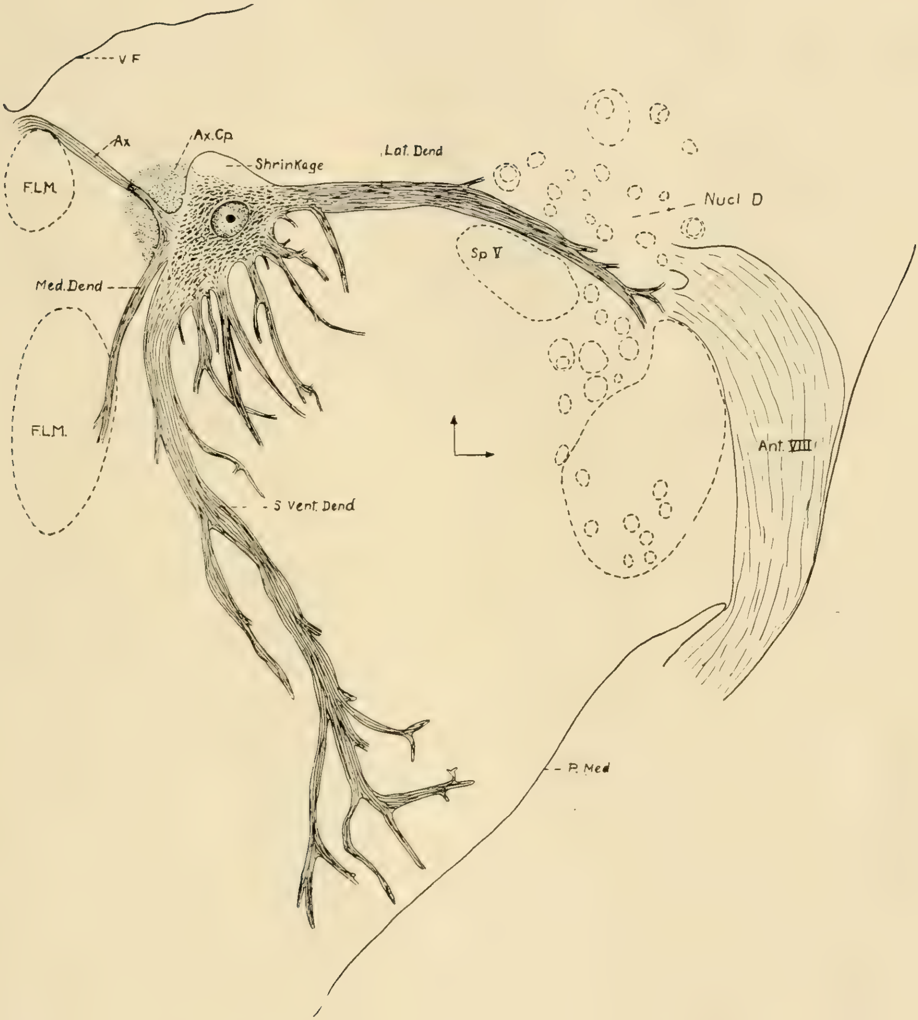
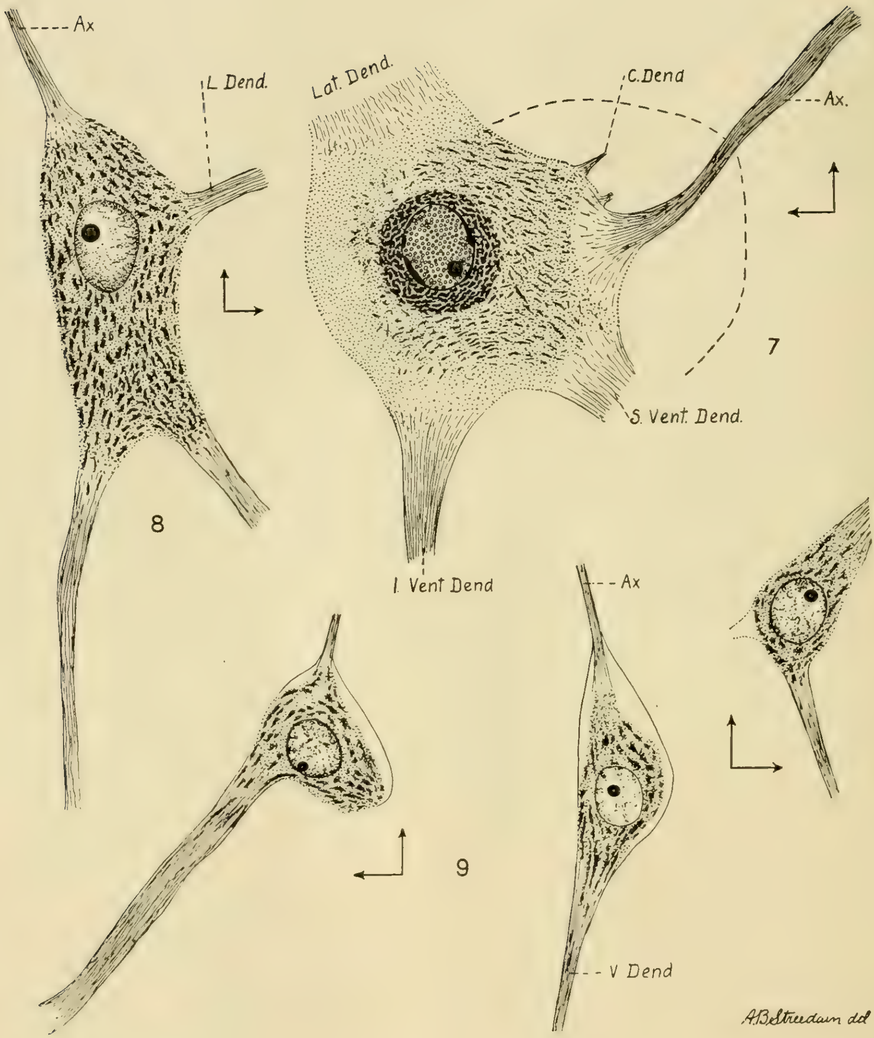


Fig. 6 From the brain of a larval Salmo clarki 32 mm. long, fixed in formol-Zenker and stained with toluidin blue and erythrosin. A reconstruction of Mauthner's cell from a transverse series of 20 sections each 10 μ in thickness, magnified 250 diameters; to show the relatively small nuclues, the character of the Nissl substance, the great girth of the lateral and ventral dendrites (fig. 11) and the relations of the lateral dendrite to Deiters' nucleus and the VIIIth nerve roots.



Figs. 7–9 Drawn from the brain of an adult Ameiurus melas 12 cm. long, stained with toluidin blue and erythrosin, magnified 630 diameters to show the relative sizes of a Mauthner's cell, a Müller's cell and the large cells of the nucleus motorius tegmenti and the similarity of the Nissl bodies in all three types.

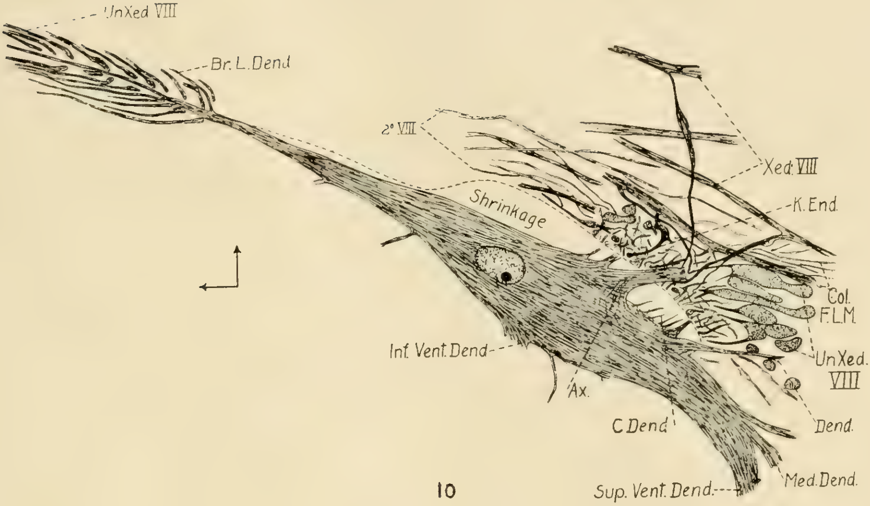


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Fig. 7 The left Mauthner's cell drawn from two consecutive 10 μ sections. Both Mauthner's cells in this brain were apparently regenerating their Nissl substance; the peripheral Nissl bodies are small and faintly stained, a zone of large deeply stained flakes completely surrounds the nucleus and a layer of chromatin lines the nuclear membrane. The extent of the axone cap is indicated by the broken line on the medial side of the cell.

Fig. 8 One of the Müller cells of the right pars superior of the nucleus motorius tegmenti. This cell is indicated by the guide line *Mül. C.* in figure 2. The lateral dendrite was large and well developed.

Fig. 9 Three cells from the pars superior; one was taken from the left side the other two from the right, as is indicated by the arrows. The clear area between the solid line and the protoplasm of the cells is a shrinkage space. The nuclei are relatively large as compared with the Mauthner's and Müller's cells.

Fig. 10 Part of the left Mauthner's cell from the brain of a 50 mm. Ameiurus larva prepared by the Cajal method. A combination of five sections, 8 μ thick, drawn with a Zeiss 2.0 mm. apo., oc. 6, and reduced to 600 diameters magnification. The series was cut in the plane of the lateral dendrite to show the terminations of the VIIIth root fibers upon it. These endings and the axone cap are the only parts of the pericellular net shown and the details of both types are drawn from single sections. The appearance of the two synapses in the silver preparation should be compared with that shown in figures 11, 12, and 13, which are taken from osmic-Zenker material.

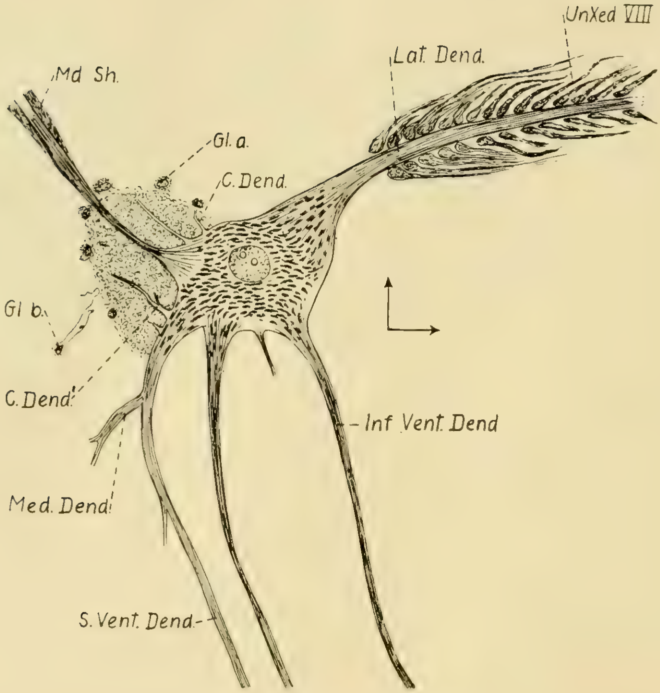

Fig. 11 The right Mauthner's cell from a young Ameiurus melas, fixed in formol-osmic-Zenker and stained with iron hematoxylin. A semidiagrammatic reconstruction from ten sections, 5 μ thick, magnified 250 diameters to show the relations of dendrites and axone to the cell body and the two striking synapses of the cell, viz., the endings of the VIIIth root fibers (*UnXed VIII*) upon the lateral dendrite and the axone cap covering the medial surface of the cell. Only four of the cap dendrites (*C.Dend.*) are shown.

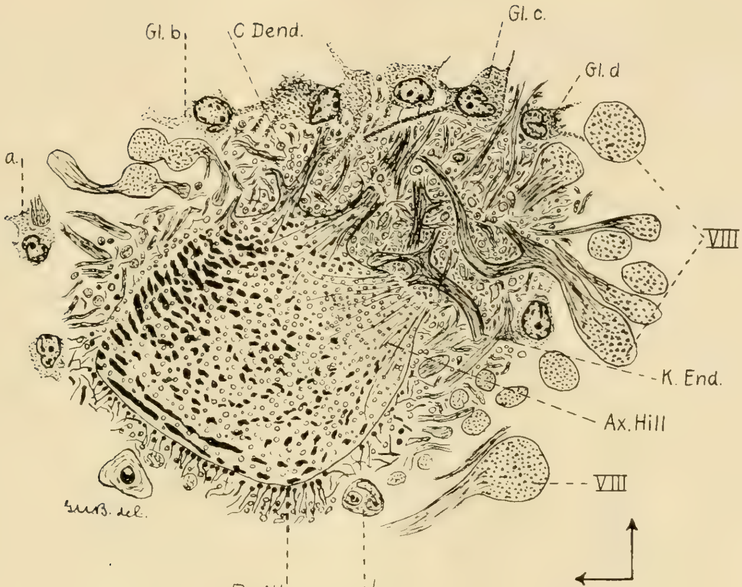

Fig. 12 The detail of the axone cap and of the pericellular net of Mauthner's cell drawn from a single section of the same brain as figure 10, but taken from the left Mauthner's cell, Zeiss 1.5 mm. apo., oc. 4, reduced to 788 diameters. The section cuts the base of the axone hillock obliquely and to one side of the nucleus. The axone cap is shown to be made up of collaterals of nerve fibers, dendrites of Mauthner's cell (*C.Dend.*) and processes of glia cells (*Gl.*). There is no indication of the fusion of nerve fibers in the dense neuropil.

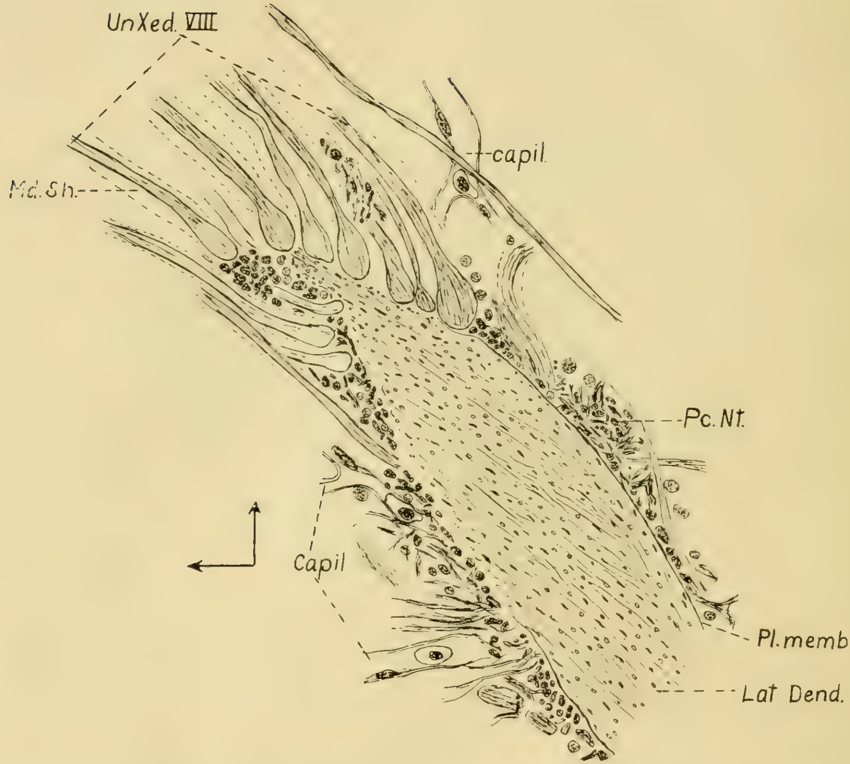

Fig. 13 The detail of the VIIIth endings and pericellular net of the lateral dendrite of Mauthner's cell, drawn from a single section of an adult Ameiurus brain fixed in osmic-Zenker and stained with iron hematoxylin. Zeiss apo. obj. 1.5 mm., oc. 4, reduced to 788 diameters. The section passes obliquely through the base of the lateral dendrite and shows the bulb-like endings of the VIIIth root fibers, and the fine meshed neuropil of the pericellular net on its surface.

A NOTE ON THE SULCUS LUNATUS IN MAN

DAVIDSON BLACK

From the Central Dutch Institute for Brain Research in Amsterdam and the Anatomical Laboratory, Western Reserve University, School of Medicine, Cleveland, Ohio

THREE FIGURES

Through the courtesy of Dr. Ariëns Kappers, I am able to record here a very beautiful example of a sulcus lunatus occurring in a new-born European babe, from the collection of the Central Dutch Institute for Brain Research.

While recognizing that the occurrence of a sulcus lunatus in some form is frequent rather than exceptional in European brains, justification for the publication of the present note lies in the fact that the description of this typical specimen affords an opportunity for making certain preliminary remarks which appear necessary through the publication by Dr. van Valkenburg (1) of his views on this sulcus. The case is but one of those which have come under observation in the course of an investigation on the subject of the sulcus lunatus, the data and the results of which, should they warrant such action, it is proposed to publish at a later date.

This specimen, more especially on the left side, presents a typical picture of the general morphological relations of the human lunate sulcus (figs. 1 and 2).

On the right side (fig. 3), the caudal end of the interparietal sulcus (B.N.A.) is joined to a furrow which passes in a sagittal direction behind the mesial edge of the sulcus lunatus. In other words, the sulcus occipitalis transversus does not lie wholly in front of the lunate sulcus as is usually the case.

On both sides the sulcus praelunatus is small, but its course frontad between the lateral extremity of the transverse occipital furrow and the mesial side of the sulcus occipitalis inferior, leaves no doubt as to its identity.

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Kappers (2) has shown that the relations obtaining between the lunate and transverse occipital sulci are such as to give rise to two distinct varieties of pattern in this region.

In one variety the occipitalis transversus is not connected with the sulcus lunatus, which is the common condition in Ateles (and Cebidae), and thus has been termed the 'Ateloid condition.' The second variety is characterised by a more or

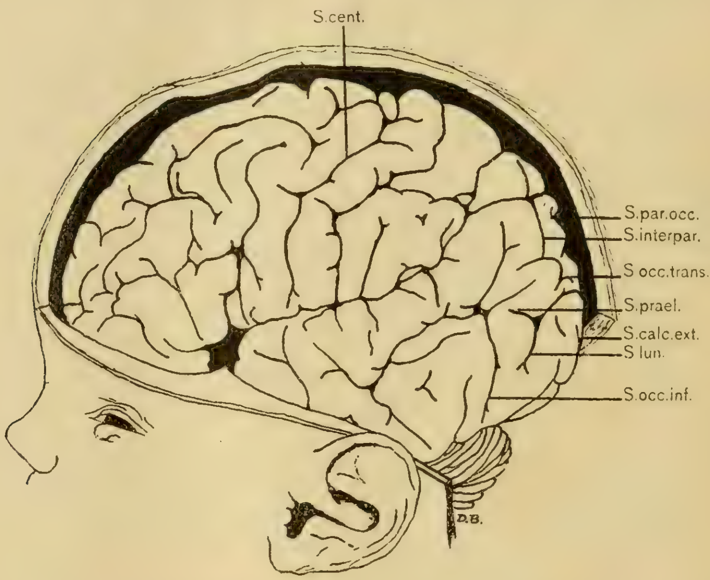

Fig. 1 Lateral view of the left side of the cerebrum of a new-born babe, exposed *in situ*. *S. cent.*, Rolandic sulcus; *S. lun.*, sulcus lunatus; *S. interpar.*, pars intraparietalis of sulcus interparietalis (B. N. A.); *S. occ.*, sulci occipitales; *S. occ. inf.*, sulcus occipitalis inferior; *S. occ. trans.*, sulcus occipitalis transversus; *S. par. occ.*, sulcus (fossa) parieto-occipitalis; *S. prael.*, sulcus praelunatus.

less complete fusion between the lunate and transverse occipital sulci such as usually obtains superficially in the anthropoid apes. On this account Kappers has termed the second variety the 'Anthropoid condition.' In the specimen here recorded it is evident that the 'Ateloid condition' obtains.

Van Valkenburg, in his most interesting paper on the sulcus simiarum in man (1), has enumerated certain definite conditions

to which a fissure must conform in order to be recognized as an indubitable sulcus lunatus. In order to discuss this question more fully I will review shortly the opinions that have been expressed by recent investigators on this subject.

In 1903 Elliot Smith described a sulcus in the human brain, homologous to the so-called 'Affenspalte' of apes, to which he gave the name 'sulcus occipitalis lunatus' (3). The evidence

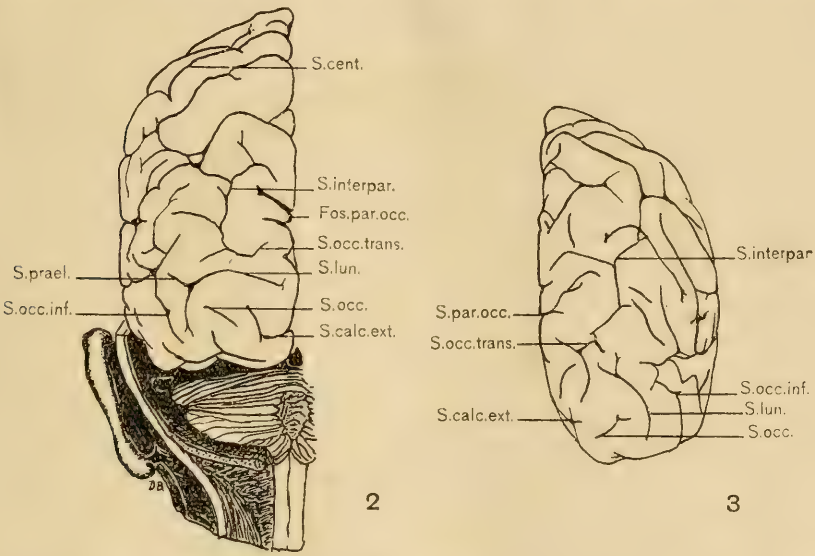

Fig. 2 Same preparation as in figure 1 seen from behind. *S. calc. ext.*, lateral calcarine sulcus; *fos. par. occ.*, fossa parieto-occipitalis, in which is seen the exposed summit of the gyrus intercuneatus. Other lettering as in figure 1.

Fig. 3 Posterior view of right cerebral hemisphere, which was exposed by a later dissection. Lettering as in figures 1 and 2.

upon which this conclusion is based is twofold: first on account of the essential similarity of the sulcal pattern in certain primitive Egyptian brains and in the brains of the great anthropoids; and second because in apes the lunate sulcus forms the definite anterior limit of the area striata on the lateral surface of the occipital region, while in the Egyptian brains, though not invariably the case, this condition is not infrequently met. Since that time a very voluminous literature, much of it being of a

controversial nature, has accumulated upon the subject of this homology.

Reference to the further work of Elliot Smith (3 to 9) and also to the contributions of Zuckerkandl (10 to 13), Kappers (op. cit. supra), van Valkenburg (op. cit. supra) and others, makes it clear that the crux of this controversy lies in the recognition of what constitutes the essential features of the sulcus lunatus in apes. Only after these have been established can one broach the subject of its homology with the lunate sulcus in man.

In his report cited above (q. v.), Kappers has considered this question carefully, and concludes, with Elliot Smith and Brodmann, that the sulcus lunatus represented in apes by the bottom fissure of the deep fossa simiarum, is homologous with the fissure of the same name frequently found on the lateral surface of the occipital region in man.

The points, to which I have already alluded, upon which van Valkenburg (q. v.) bases his diagnosis of the sulcus lunatus may be quoted as follows:

(1) "The sulcus in question lies somewhat crescent-shaped (with its concavity caudad) or more transversal, not far from the pole of the occipital lobe;"

(2) "In its lateral part terminates a sulcus, that is often connected with the first temporal sulcus (sulcus praelunatus);"

(3) "More or less parallel to it, more towards the front, lies a sulcus, into which the sulcus interparietalis terminates (sulcus occipitalis transversus);"

(4) "The occipital extremity of the sulcus calcarinus falls (whether bent or not round the mantle-side) behind it, and sometimes extends between two sulci occipitales which are found there (these may be connected V-shaped)."

In the above scheme, no mention is made of the relation of the sulcus lunatus to the area striata. Indeed this observer does not regard the relation of this area to the lunate sulcus as "a point of issue for proving homology," as Elliot Smith has done and it is to this I wish to draw attention.

As a reason for his opinion van Valkenburg cites the well known fact that the stria of Gennari in most cases does not ex-

tend so far forward as the sulcus lunatus in man, thus this sulcus does not limit the striate area frontally. In explanation of this fact he refers to the findings of both Ziehen (14) and Kappers (op. cit.), who have shown that the sulci are more conservative in their migrations than the neighboring cortical zones.

The key to the situation may be found in the last statement. The striate area is pushed backward during the evolution of the distinctively human parieto-occipital 'association' fields. The more conservative lunate sulcus, if it survive at all in the altered conditions of cortical tension attendant upon this unfolding process, does not accurately follow the retreating area striata. However, it is to be noted that the more operculated the lunate sulcus be (e.g., the more successful it has been in retaining its original anthropoid shape amid the changing human conditions), the nearer does the striate area approach its lip. The very fact that the area striata *never* extends beyond this sulcus, but *does sometimes* terminate at its lip, even in Europeans, makes the distribution of the stria of Gennari a most important point in this issue.[1]

I would thus advocate the addition to van Valkenburg's list of a fifth and most important criterion—one emphasised by Elliot Smith from the outset, viz: The area striata never extends beyond the sulcus in question, though it may fall short of it, for reasons already noted; and its forward extension is in direct relation to the degree of operculation.

January 31, 1915.

[1] I have seen the area striata extend to the lip of the lunate sulcus in two specimens obtained at autopsy this autumn—both sulci were on the right side and both subjects were adults of American parentage and of European extraction.

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A NEW FISH BRAIN FROM THE COAL MEASURES OF KANSAS, WITH A REVIEW OF OTHER FOSSIL BRAINS

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NINETEEN FIGURES

CONTENTS

I. INTRODUCTION

The preservation of the soft parts of extinct animals has always been a matter of great interest to students of paleontology and there have appeared on this subject a number of papers which have been reviewed and listed by the writer ('11) in a previous contribution on the soft anatomy of fossil vertebrates. The exact manner in which the softer structures are preserved varies in different cases. They may be carbonized,[1] mummified,[2]

[1] Reiss, Otto. 1895. Archiv f. mikros. Anat., Bd. 41, p. 492; Bd. 44, p. 89. Discusses theories of fossilization. Dean, Bashford. 1904. Amer. Geol., vol. 30, pp. 273–278. Critical discussion of Reiss' views concerning the conditions of fossilization. Dean, Basford. 1909. Mem. Amer. Mus., Natl. Hist., vol. 9, pt. v, p. 234. Figures and discusses the histological structure of the muscle and kidney of a Devonian shark.

[2] Osborn, H. F. 1912. Mem. Amer. Mus. Nat'l. Hist., N. S., vol. 1, pt. II, p. 33, with plates. A mummified dinosaur is described from the Cretaceous in which the skin, the epidermal pattern and muscle are preserved.

or changed into a variety of mineral substances, such as kaolin,[3] or phosphate (Eastman, '08); or the form of the part may be retained by a cast of the cavity (Scott, '98), which the organ occupied. The latter is the manner of formation of the specimens of reptilian and mammalian brains described in the papers listed in the appended bibliography.

The study of the brain cast of a mammal would give a more accurate idea of the anatomy of this organ than would the cast of the brain cavity of a reptile, since the brain in mammals more nearly fills the brain case (Osborn, '12) than it does in reptiles,[4] as noted by Dendy in the brain of Sphenodon. The cast in either case is of the dural cavity and gives only an approximate picture of the actual configuration of the brain of the animal, whether reptile or mammal, since the smaller convolutions make no impression of the inner surface of the skull (Scott, '98, p. 374), even in man. If the brain of man were known only from the cast of the fossil crania, the greatly convoluted nature of the cortex would never be suspected (Gregory, '14, fig. 8). On this account a study of brain casts is attended with considerable uncertainty with respect to the value of all the characters. This has been overcome to some extent recently by Palmer ('13) in his careful interpretations of brain structures of a fossil ungulate (Anoplotherium) from the Eocene of France.

The subject of Paleoneurology is still in its infancy. The earlier and pioneer publications dealt with the most obvious features of the specimens at hand, from which, to be sure, many interesting and important generalizations were made. There is still much work to be done, however, from a strictly anatomical standpoint which will without doubt be of the greatest service in interpreting the relationships of the animals of the past.

[3] Moodie, Roy L. 1910. Amer. Nat'l., vol. 44, p. 367. Discusses the conversion of bone into kaolin and describes the preservation of a complete alimentary canal of a branchiosaur from the Coal Measures.

[4] Dendy, A. 1911. Phil. Trans. Roy. Soc. Lond., Ser. B, vol. 201, pp. 227–331.

II. FOSSILIZATION OF FISH BRAINS

The soft parts of fossil vertebrates have been replaced in a few cases by slow infiltration of mineral substances just as skeletal structures are fossilized by replacement of osseous substance by minerals. Such has been the apparent method of preservation of the small brains from the Coal Measures, described in this paper, as well as the brains of Rhadinichthys described by Eastman ('08) from the Mississippian of Kentucky. In regard to the manner of preservation of these brains, Eastman ('08, p. 269) says:

> * * * It is evident that we have here to deal with a veritable brain-structure the substance of which became transformed into calcium phosphate before decomposition could set in, and whose walls in consequence are scarcely shrunken. This view is further confirmed by the presence of nerve fibers and blood vessels, slightly enlarged in some cases, it is true, by the segregation of mineral matter, but coinciding in position with altogether similar nervous and vascular structures in modern ganoids and bony fishes.

The precise manner of formation and preservation of the fossil fish brains has never been determined, so far as I am aware. Much work has been done, it is true, on the formation of phosphatic nodules (noted by Eastman, 1908, footnote, p. 266) and it is possible that the brain substance has been replaced by a slow infiltration of calcium phosphate; although such a replacement is very difficult of comprehension in view of the chemical analysis of the brain, which, as ascertained by Waldemar Koch[5] for the human brain, contains a very high percentage of water, and a smaller but appreciable amount of soluble substances. The amount of water in the brain is much greater among the lower vertebrates. Doctor Donaldson writes me that his tables show 84 to 85 per cent for the proportion of water in the brain of the common frog, Rana pipiens; 76 to 78 per cent in the entire brain of the summer flounder at Woods Hole. Observations on the brain of the albino rat show 88 per cent at birth and 78 per cent at maturity. George G. Scott[6] gives a range of 75.5 to 83 per cent according to age in the selachian, Mustelus canis.

[5] Amer. Journ. Physiol., vol. 11, no. 3, p. 326.

[6] Scott, George G. 1913. Annals N. Y. Acad. Sci., vol. 23, p. 52.

I have been unable to find any account of an analysis of fish brains; and am thus uncertain as to the relative amounts of resistent substances, such as neurokeratin.

The brain case in all recent selachians and teleosts is very much larger than the brain itself. In the skate, Raja binoculata, from Puget Sound, for example, the size of the brain cavity is out of all proportion to the size of the brain, which occupies only a small part of the space. We may safely assume that the brain case of Paleozoic fishes was similar in this respect, since we find such a general similarity in other characters. We must thus account for the beautiful preservation of the brain and the complete disappearance of the skull of the Coal Measures fish in some other way than by assuming that a cast of the brain case was formed before the dissolution of the partly osseous, partly cartilaginous skull. It is hardly conceivable that the brain was preserved by a sudden filling of the brain cavity and a subsequent infiltration of the space occupied by the brain, after the dissolution of that organ.

III. REVIEW OF FOSSIL SENSORY STRUCTURES

It is the intention of the following pages to review the work done on fossil brains, to give a detailed account of the anatomy of the brain and ear of a small ganoid (?) fish recently discovered in shales near Lawrence, Kansas, and to append a bibliography of papers dealing with fossil brains and other neural structures. The plan of this review will be to proceed upward in geological succession from the earliest formation in which are found traces of sensory organs sufficiently well preserved to afford any knowledge of their structure. This will also be proceeding upward from the most primitive known vertebrates to the higher mammals. The following outline will facilitate an understanding of this review.

Devonian	Ostracoderms—traces of brain cavity, lateral and pineal eyes; sensory (lateral line) grooves (Patten, '12) Selachians—Lateral line, muscle, kidney, skin (Dean, Mem. Amer. Mus. Natl. Hist., vol. 9, pt. v, 1909) Arthrodires—Sensory (lateral line) grooves on cephalic plates (see Dean. Mem. N. Y. Acad. Sci., vol. 2, Pt. III, '01, pp. 116–119)

Mississippian.......	Actinopterygians (ganoids)—Nearly complete brain, ear, nerves, and arteries of Rhadinichthys deani (Eastman; '08)
Pennsylvanian......	Fishes with traces of lateral line
	Actinopterygians (ganoids) (?)—Complete brain, inner ear blood vessels, and nerves
	Amphibians—Lateral line canals of head and sensory structures of lateral line organs on side of body and tail; complete alimentary tract and muscle fibers (Journ. Morph., 1908, p. 511)
	Reptiles—No sensory structures represented
Permian............	Fishes—No sensory structures preserved
	Amphibians—Brain case and nerve foramina; lateral line grooves on skull and pineal opening (Jour. Morph., '08, p. 511)
	Reptiles—Brain case, nerve foramina, dural cast of brain and inner ear (Case, '97)
Triassic.............	Fishes—Lateral line organs (Bull. 18, Conn. State Geol. Natl. Hist. Survey, '11)
	Amphibians—Cast of brain (?), lateral line canals on skull (Wiedersheim, '78; Jour. Morph., '08, p. 511)
	Reptiles—Brain of Belodon (Cope, '88)
	Mammals—No sensory structures known
Jurassic.............	Fishes—Lateral line organs as indicated on the body scales
	Amphibians—No sensory structures represented among the two or three known species
	Reptiles: Pterodactyls—Brain and ear of two species
	Reptiles: Dinosaurs—Dural casts of brain and sacral intumescence
	Birds—Archaeopteryx is the only possibility
	Mammals—Nothing known
Cretaceous..........	Fishes—Peculiar lateral line of a selachian (Woodward)
	Amphibians—No sensory structures represented in the few species known
	Dinosaurs—Complete dural casts of brain of Tyrannosaurus (Osborn, '12)
	Birds—Brain of toothed bird, Hesperornis (Marsh, '80)
	Mammals—Nothing known
Eocene to Pliocene (age of mammals).	Dural casts of the brain of many orders of mammals described in papers listed in bibliography. The cerebellum in all preponderantly large, with cerebrum apparently smooth, though this latter may be due to the fact that the dural cast does not copy the entire series of convolutions of the cortex.
	Dural cast of calvarium of Pithecanthropus erectus and more complete dural cast of Eoanthropus dawsoni.
Pleistocene..........	The most interesting information is in regard to the cranial capacity of the extinct species of man Homo neanderthalensis (Boule. Annales de Paleontologie, tome 6).

There is probably a large amount of material preserved in the various collections of fossil vertebrates which will add greatly to our knowledge of the anatomy of the neural structures of vertebrates when this material has been carefully studied. Only a few partial attempts have been made to derive the optimum of information from the fossil material. Many features, most interesting from an anatomical standpoint, are barely mentioned in the description of species which has occupied so large a place in the paleontological work of the past.

IV. SENSORY STRUCTURES OF THE OSTRACODERMS

The most primitive vertebrate-like animals in which any indications of sensory structures have been preserved is Bothriolepis from the Devonian of Canada and Pennsylvania, one of the best known representatives of the fish-like Ostracoderms. Traquair[7] has described some curious fishes from the lower Devonian of Gemünden in which there are traces of sensory structures, such as sensory grooves and eyes. The following discussion of the neural structures in the Ostracoderms I owe to Professor William Patten of Dartmouth College, and the figures will be readily recognized as due to his well-known skill. The discussion which follows is taken verbatim from a letter written by him January 8, 1915:

At your request I am sending you two outline sketches of the head region of Bothriolepis, showing the probable size and location of the brain and principal sense organs. You are at liberty to make use of them and the accompanying notes as you see fit.

It is, no doubt, worth while to put such data as are available into visible concrete form, although it is obvious that the presence of a large personal factor in reconstructions of this character is inevitable. However, if that fact is duly recognized, it is not likely that any harm will be done thereby.

Let me say at the outset that no trace of a brain could be found in our dissections of the head, or in the numerous cross and longitudinal sections that were made through it. But these fossils, as you know, are so beautifully preserved, that the exact form of the head, and the minute structure and relations of all the hard parts could be determined

[7] The lower Devonian fishes of Gemünden. Trans. Roy. Soc. Edinburgh, vol. 40, pt. IV, pp. 723–739, with plates.

with great accuracy and certainty. The parts that are preserved give us certain fixed points that enable us to determine the size and location of the brain with a reasonable degree of certainty. The general form of the brain and the direction of the principal nerves may be inferred from the size and location of the principal sense organs and viscera. These fixed points are as follows:

(1) A small vertical ethmoidal plate (figs. 1 and 2, *e*) lies between the olfactory openings and extends almost to the inner shelf of the rostral plate. The forebrain probably extended well up to this plate but not beyond it.

(2) The two small olfactory openings just in front of the lateral eyes, indicate the presence of paired olfactory organs, of small size, lying on either side of the ethmoidal plate, in the chamber formed by the inner and outer shelves of the rostral plate (figs. 1 and 2, *ol.o*).

(3) A deep, clean-cut, conical cavity on the inner surface (of the) middle occular plate, and a pronounced lens-like swelling on its outer surface indicates the presence of an exceptionally large and well-developed pineal eye (figs. 1 and 2, *p.e.*). Caudad to it are two other pit-like depressions on the inner surface of the semilunar post-occular plate, indicating the presence of two other similar organs (figs. 1 and 2, *p.e.'*).

(4) Two small pores in the occipital plates mark the location of the openings to the endolymphatic ducts (figs. 1 and 2, *d.e.*) and indicate the presence of underlying auditory vesicles (figs. 1 and 2, *au.*).

(5) In sagittal sections, a blackened band (fig. 2, *b.pl.*) extending backwards from the inner shelf of the rostral plate probably represents the floor of a cartilaginous endocranium.

(6) The stomach and gills are located in the large posterior chamber.

(7) A pronounced hinge joint marks the line separating the branchial and visceral region from the head proper, in which the brain, jaws and principal sense organs are located.

(8) Two median bony processes extend inwards from the roofing plates of the branchial region that served for the support of the muscles and tough connective tissue. The spinal cord probably lies just below the blackened remnants of these tissues. No trace of a notochord or vertebral column could be found.

All these characters enable us to locate the brain within the chamber between the floor of the endocranium and the occular plates, and indicates that the brain had a form and location like the one shown in the restoration (fig. 1). The location of the median and lateral eyes and the olfactory organs, in a compact group, on the dorsal surface is suggestive of the cyclostomes.

The anatomy of this form (Bothriolepis) with suggestions as to its phylogenetic significance are given fully in Professor Patten's work[8] to which reference has been made for the condition

[8] The evolution of the vertebrates and their kin. Philadelphia, 1912.

of the sensory (lateral line) grooves which he refers to as 'cutaneous sense organs' (loc. cit., p. 356, fig. 236.). He says: "The prevailing position of the lateral line organs on the neural surface of the head, where they are out of touch with the food or surrounding objects, is only intelligible on the assumption that they represent the remnants of the gustatory and tactile organs that were located on the neural surface of the head, in their arachnid-like ancestors" (loc. cit., p. 358).

V. THE BRAIN AND EAR OF RHADINICHTHYS, A MISSISSIPPIAN GANOID

The fish-bearing nodules described by Eastman ('08) from the base of the Waverly (Mississippian) of Boyle County, Kentucky, are entirely similar to those described below from the Coal Measures of Kansas. Doctor Eastman has very kindly sent me the original photographs of the nodules (fig. 3) in which the brains are preserved, from which the line drawing (fig. 4) is prepared. The anatomy of the brain of Rhadinichthys is quite similar to that of the fishes from the Kansas Coal Measures as may be seen by reference to the figure (fig. 4). Eastman says ('08, p. 267) in regard to his discovery: "An entirely new chapter in the anatomy of extinct animals is opened by the discovery of the actual phosphatized brain, internal ear, and blood vessels of a Paleozoic vertebrate, such as are clearly revealed by the contents of these fish-bearing nodules from the base of the Waverly in Kentucky."

The similarity in structure between the brain of Rhadinichthys and that of the undetermined fish from the Coal Measures of Kansas is very striking. The optic lobes in both are very large, and the general proportions are very similar. The median portion of the Mississippian specimen is broken so as to obscure that portion of the lobe, and to leave it uncertain as to the presence of the median elevation which is so well shown in the Coal Measures fish (fig. 15). The lateral cerebellar lobes are almost precisely the same in appearance and location and in the Mississippian fish are well preserved. The median ends of the lobes are more nearly approximated than are the same por-

tions of the lobes in the Coal Measures fish. There is no indication of the structure which, in the Coal Measures fish, has been interpreted as a median encephalic vein (at first interpreted as a pineal body). In the region just posterior to the lateral cerebellar lobes there is considerable difference in the structure of the brains. In the Mississippian fish there are four distinct elevations, the most anterior two of which may be interpreted as non-involuted portions of the cerebellum (fig. 4), though it is much more probable that they are the anterior portions of the tuberculum acusticum. There is a well marked median sulcus between the two elevations, a continuation of the sulcus dividing the lateral lobes of the cerebellum. There is no indication of the tubular elevation as seen in the Coal Measures fish. Just posterior to these two lobes and divided from them by a slight transverse sulcus lie two smaller lobes, similar in general appearance to the anterior ones which have been interpreted as anterior lobes of the tuberculum acusticum. These posterior lobes are tentatively interpreted as posterior portions of the tuberculum acusticum. It is unfortunate that the posterior portion of the brain is lost and it is to be hoped that Doctor Eastman will illustrate this portion of the anatomy for us from the additional material in his possession. The vertical semicircular canals follow the same course in the two forms and have the same relations. A lateral portion of the ear of the Mississippian fish is preserved, which I suppose is the ampulla of the horizontal semicircular canal. It is present on both sides of the brain (fig. 4) and, if it is correctly interpreted, the ampulla lies much more lateral in the Mississippian than in the Coal Measures brain.

The specimens studied by Eastman were submitted to Parker ('08) who studied them and corroborated Eastman's observations as follows: "On the right-hand side the anterior vertical canal is well preserved throughout its whole extent from the apex of the superior sinus of the utriculus to the anterior ampulla. Doctor Parker was especially interested in the ear as preserved in the several nodules submitted to him and the greater part of his discussion is devoted to this organ. He also discusses the

presence of what "corresponds to the basilar artery, the large ventro-lateral branches to the carotid arteries, and the smaller branches to those vessels which in fishes are distributed to the ventral and lateral surfaces of the brain." One of the specimens studied by Doctor Parker is figured herewith; the present figure being taken from a photograph published by Eastman ('08), pl. 13, fig. 8), which has been very kindly sent me by him.

Anterior to the optic lobes, in the Mississippian fish (fig. 4) lies an elevation exactly comparable to what in the Coal Measures fish has been interpreted as the 'thalamus.' Its superior surface is much broken so that its entire extent is uncertain, although its general form seems to be that of the Coal Measures fish (fig. 6). Still anterior to this structure lies the olfactory tract which is broken from one side but is indicated on the other (fig. 4). This structure is apparently quite different from the Coal Measures fish in the distinct separation of the two tracts, more nearly resembling in this respect the carp[9] than it does the Coal Measures fish. This one point would cause one to hesitate to ally the fishes from the Coal Measures with those from the Mississippian, as has been done below. In general proportions and size, the major parts of the brain are the same. Whether these latter points are of more importance in relationship than the condition of the olfactory tract, the writer is uncertain. It is possible that if more of the olfactory tract in the Coal Measures fish were preserved there would be a more general similarity than at present appears.

The specimens from Kentucky are, apparently, much more thoroughly phosphatized than are those from Kansas. Certainly the latter are much more perfectly preserved, since the small brains from the Kansas Coal Measures far surpass in the beautiful preservation of anatomic detail anything so far described.

The chief interest in the close resemblance in structure between the brains of these fishes lies in our ability to arrive at some conclusion concerning the zoölogical position to which we may assign the fossil brains from the Coal Measures of Kansas. East-

[9] Sheldon, R. E. The olfactory tracts and centers in teleosts. Jour. Comp. Neur., vol. 22, 1912, pp. 177–339; see especially plate 1.

man ('08) has regarded Rhadinichthys as a member of the ganoids with certain teleostean affinities, and has classed it as follows: Order—Actinopterygii, Suborder—Chondrostei (sturgeons), Family—Palaeoniscidae. The Coal Measures fish will probably find its affinities somewhere in this grouping.

Since it is probable that the history of these fishes is not generally known to the readers of this Journal, it will be well here to point out some of the chief facts concerning the geological occurrence of the Chondrostei (sturgeons) and give a short discussion of the characters of the family Palaeoniscidae.

The Chondrostei are the oldest and most primitive of the Actinopterygii and are first represented in the Lower Devonian by a Palaeoniscid genus, Cheirolepis, a contemporary of the earliest Crossopterygii. They occur throughout the Mesozoic and continue scantily represented in later periods, to be represented by their degenerate descendants of today, the sturgeons and paddle fishes.

The family Palaeoniscidae is characterized by Eastman ('08) as:

> Primitive Chondrostei with fusiform bodies, short dorsal and anal fins, and usually with a complete investment of articulating rhombic, rarely cycloid, ganoid scales. Fulcra generally present at the bases of the median fins, and especially along the dorsal border of the upper caudal lobe. Ribs are not known to be present. Skull invested by a very complete series of paired dermal bones, which in number and disposition conform to the normal Teleostome type. The secondary upper jaw includes both premaxillae and large maxillae; and, as a rule, both the dentary and splenial bones of the lower jaw are dentigerous. Except for the absence of an interoperculum, the opercular series of bones is complete, including numerous branchiostegal rays. There is a single small median jugular plate.

The above discussion is of interest further in that, in all probability, the fish brains from the Coal Measures of Kansas described below belonged to representatives of the Palaeoniscidae. There are a few opercular elements preserved in nodules associated with the nodules containing the brains, but their association with the same fish is so uncertain that it is best to leave the question an open one.

VI. THE BRAIN FROM THE COAL MEASURES

Aside from the discovery of fossil brains reported below, nothing is known of the neural anatomy of the vertebrates from that great series of strata known collectively as the Coal Measures (Pennsylvanian). Among the Amphibia of that series the author has described the complete alimentary canal of three specimens of Eumicrerpeton parvum, a small salamander from the Coal Measures of Illinois[10] and muscle fibers of another species, Tuditanus walcotti[11] a microsaurian from the Coal Measures in Ohio. Among the fishes many authors have recorded their observations of body outlines[12] and other firmer structures.

The specimens, among which are found the little fish brains, were collected in shales just above the Kickapoo limestone in the Coal Measures one mile east of Lawrence, Kansas, by Doctor W. H. Twenhofel and Carl O. Dunbar of the University of Kansas, to whom I am indebted for the privilege of studying these interesting remains. They have recently[13] described this deposit in some detail on account of its interest from a geological standpoint. The writer has had in his possession for some years similar nodules collected in shales near Baldwin, Kansas. When these nodules were first examined the thought occurred that they contained fossil brains, but since they were not known to be such and since the material was rather fragmentary they were not described. A re-examination indicates a great similarity to those described below. Remains of the ear, arteries, or veins, brain structures and other points of interest are to be seen in these nodules. The brain structures indicate a fish like the larger ones from near Lawrence. The specimens are, however, much more poorly preserved than are the ones figured herewith. The objects, presently to be described, are all encased in small phosphatic nodules, few of them measuring over 1 inch in diameter. The fossils have formed a plane of weakness along which the

[10] Amer. Nat'l, 1910, vol. 44, p. 367; Kansas Univ. Sci. Bull., 1913, vol. 6, no. 2, pls. 3, 5, 6.

[11] Proc. U. S. Nat'l Museum, vol. 37, p. 16, pl. 7.

[12] Eastman, C. R. 1902. Journ. Geol., vol. 10, p. 538, with figures.

[13] Amer. Journ. Science, vol. 37, August, 1914, p. 157.

nodules split when struck with the hammer. The stone surrounding the fossil is relatively soft and may easily be worked with a sharp tool (fig. 5). In this way were exposed the structures shown in figures 15, 16 and 17.

There are a dozen or more nodules which exhibit the brain in varying degrees of perfectness. The two figured (figs. 15–17) are the best preserved and they are the ones which first called attention to the possibility of their neural nature. The following description is based in large part on these specimens. Among the brains in my possession there are two which present characters at variance with the type brains. Whether this is due to variation in the species or whether these characters represent another form I am not sure. One of the brains has become loosened from the nodule so that we may study its characters from all sides, as was noted by Eastman ('08), p. 267, fig. 40 b) for the brain of Rhadinichthys. Four specimens show the semicircular canals beautifully.

The brain as a whole may be best understood from an examination of the figures (figs. 15–17). The entire length of the best preserved and most complete brain is 15 mm. Its height is 6 mm. The optic lobes measure 5 mm. in median length. The figures were all made by Mr. Tom Jones, who carefully measured the various parts of the brain with fine pointed calipers and determined the dimensions on a divided millimeter scale so that the proportions are correctly shown; the magnification under this system of measurement being easily determined.

There is no modern fish so far known with a brain sufficiently comparable to the Coal Measures brain to allow a direct comparison. On the advice of Professor C. Judson Herrick, to whom I am indebted for advice and help throughout the entire course of this investigation, I have described the brain independent of any attempt to compare it directly with modern fishes, although a few references are made to the literature of modern fishes in cases where the several parts of the brain seem to call for such comment. This wide separation in structure from modern fishes may be due to the degree of evolution or to the environmental adaptation of the Coal Measures fish. It is difficult, if not im-

possible, to correlate correctly all parts of this fossil brain with the parts of the brain of modern fishes. We may be certain of the optic lobes, however, and some other features, such as the olfactory lobes and tracts; but other structures are not so readily determined and the interpretations placed on them are tentative. It is not possible to identify them with certainty. The form of the brains of fishes vary to suit the adaptation of the animals to their environment and, since we do not know the environment of this Coal Measures fish and since internal structure is impossible of determination, we must do what we can by tentative determination.

The *spinal cord* is only partially represented, if at all, by a short portion on the very margin of the nodule. The *vagal lobe*, which is single and median, projects backward over the fourth ventricle. In the specimen shown in figures 15 and 16 the top of the vagal lobe has been destroyed, but other specimens in which it is preserved as a mold show it as median and unpaired. In the generalized types of recent fishes the vagal lobes are developed as paired eminences in the lateral walls of the fourth ventricle, and this is the condition in all known forms of cyclostomes, elasmobranchs and ganoids. These vagal lobes, or visceral lobes, unite across the mid-plane dorsally above the ventricle immediately below the calamus scriptorius in the commissural nucleus of Cajal.[14] This is the usual condition in teleosts also, though here the vagal lobes are usually larger and more compact. In some teleosts (e.g., the catfish and other siluroids) there are two pair of these visceral lobes in front of the commissural nucleus, related respectively with the visceral sensory roots of the IX + X and VII cranial nerves. These are the vagal and facial lobes.[15] In the carp and other cyprinoid fishes these lobes are greatly enlarged and there are three separate visceral lobes in front of the commissural nucleus—a pair of very large vagal lobes, a pair of much smaller glossopharyngeal

[14] Herrick, C. Judson. 1908. On the commissura infima and its nuclei in the brains of fishes. Jour. Comp. Neur., vol. 18, pp. 409–431.

[15] For an illustration of this relation see, Herrick, C. Judson. The central gustatory paths in the brains of bony fishes. Jour. Comp. Neur., vol. 15, 1905, p. 382, fig. 4.

lobes, and a medial 'tuberculum impar,' which is formed by a fusion of the two facial lobes.[16]

In the absence of information regarding the internal structure of the vagal lobes of the Coal Measures fish, it is impossible to make safe comparisons with recent fishes. It is not improbable that this 'vagal lobe' includes the lobus VII and the lobus IX + X fused into a single dorso-medial mass, a condition not known to occur in any living fish. If this is the correct interpretation, this fossil resembles the teleosts in this region more than any known ganoid, dipnoan or elasmobranch. The brain of Rhadinichthys from the Mississippian, unfortunately, does not have the vagal lobe preserved.

Between the vagal lobe and the cerebellum in Rhadinichthys from the Mississippian are two pairs of eminences which are marked 'tuberculum acusticum' in figure 4. The same relations prevail in the Coal Measures fish, save that the members of the posterior pair are fused into a single dorso-medial eminence (fig. 15). Since we are ignorant of the internal structure and connections of these eminences, it is impossible to determine their homologies.

In recent elasmobranchs and ganoids the area acustico-lateralis, or tuberculum acusticum, which receives the VIII and lateral line roots, is represented on each side of the medulla oblongata by a thickening of the rhomboidal lip which consists of two parts. These are very clearly seen in the sturgeon, Acipenser, as described by Johnston.[17] There is a relatively undifferentiated posterior part of this thickening, which is termed by Johnston the tuberculum acusticum, and an enlarged anterior lobe immediately behind the cerebellum, the lobus lineae lateralis (lobus trigemini of Goronowitsch). The cerebellum is a thickening of the rhomboidal lip of each side immediately in front of the lobus lineae lateralis, these structures being functionally very intimately related. The relations of these parts in Necturus and

[16] See Herrick, Jour. Comp. Neur., vol. 15, 1905, p. 380, fig. 3 and p. 385, fig. 5.

[17] Johnston, J. B. The brain of Acipenser. Zool. Jahrb., Bd. 15, 1901, plate 2, figs. 5, 6, 7; also, The nervous system of vertebrates, Philadelphia, 1906, p. 16. fig. 3 and pp. 130–141.

other lower urodele Amphibia and in the larva of Amblystoma are essentially the same as in Acipenser.[18]

In teleostean fishes the area acustico-lateralis, or tuberculum acusticum, is much more compact than in ganoids and assumes a great variety of forms, in some cases being greatly enlarged. The lobes of the two sides may fuse with each other across the mid-dorsal plane above the fourth ventricle between the vagal lobes and the cerebellum. This is the condition in Gadus.[19] In Mormyrus the area acustico-lateralis is enormously hypertrophied and takes the form of two dorsal unpaired lobes, a posterior one related to the posterior lateral line nerve (vagal root) and an anterior one related to the anterior lateral line nerve (facial root). Of these the posterior lobe is the larger and has grown over the anterior lobe so that in cross section the two lobes seem to be concentrically arranged, and the whole mass appears in surface view as a single unpaired eminence, commonly termed the tuberculum impar.[20]

[18] Herrick, C. Judson. The cerebellum of Necturus and other urodele Amphibia. Jour. Comp. Neur., vol. 24, 1914, pp. 1–29; The medulla oblongata of larval Amblystoma. Jour. Comp. Neur., vol. 24, 1914, pp. 343–427.

[19] Kappers, C. U. A. The structure of the teleostean and selachian brain. Jour. Comp. Neur., vol. 16, no. 1, 1906, plate 6, figs. XCV and XCVI.

[20] Numerous figures of this remarkable teleostean brain have been published, amongst others the following:

Ecker, A. Anatomische Beschreibung des Gehirns vom karpfartigen Nilhecht (Mormyrus cyprinoides L.). Leipzig, 1854. In Ecker's figures the tuberculum impar is erroneously designated 'cerebellum.'

Sanders, A. Contributions to the anatomy of the central nervous system in vertebrate animals. Appendix. On the brain of the Mormyridae. Phil. Trans. Roy. Soc. London, Part III, no. 173, 1883, pp. 827–959. In this work the tuberculum impar is erroneously homologized with the lobus facialis of cyprinoids (a visceral sensory center which was also called tuberculum impar by the older anatomists; see p. 149.

Smith, G. Elliot. In the catalogue of the physiological series of comparative anatomy, Museum Roy. Coll. Surgeons, London, 1902, p. 103, fig. 29.

Stendell, W. Die Faseranatomie des Mormyridengehirns. Abh. Senckenbergischen Naturf. Gesell., Bd. 36, H. 1, 1914, pp. 1–39.

Berkelbach van der Sprenkel, H. The central relations of the cranial nerves in Silurus glanis and Mormyrus caschive. Jour. Comp. Neur., vol. 25, no. 1, 1915, figs. 15–19. This paper contains the first accurate and detailed description of these structures, though Stendell figured and briefly described the true relations.

In the Coal Measures fish the eminences here provisionally identified as tubercula acustica are unlike those of any of the existing Ichthyopsida, though they resemble most closely those of the teleostean species in which the tubercula acustica fuse dorsally above the fourth ventricle. The anterior eminences may correspond with the ganoidean lobi lineae lateralis, in this case crowded medialward and fused above the ventricle.

The cerebellum of the Coal Measures fish resembles closely that of Rhadinichthys from the Mississippian. Its form is unique, resembling no cerebellum known among recent fishes, though it is not far from that of the closest recent relative of these species, the sturgeon (Acipenser).[21] Dr. Johnston has suggested to me that the medial portion may be involuted between the optic lobes in the form of a valvula cerebelli, as in Acipenser and teleosts.

The *optic lobes* are teleostean in their large size, as is at once evident from an examination of the figures The eye was extremely large as indicated by the bony orbit, well preserved in a median fracture of one of the nodules (fig. 17). The orbit, as shown by the impression figured, is slightly oval and measures 8.25 mm. in antero-posterior diameter. Its large size probably accounts in part for the unusual development of the optic lobes. The relations of the optic lobes to the hypothalamus and cerebellum and their dimensions are best discerned from an examination of the figures (figs. 16, 17). The optic nerves were evidently short, as is apparently determined from an examination of the one orbital region which is at all well preserved. Apparently the optic nerve entered the orbit acentrally. The position of the *optic chiasm* has been indicated in one of the figures (fig. 16) and it is recognized by its contour on the surface of the brain. It cannot be accurately described from the present material, however, except that its position is as indicated, anterior to the lobus inferior.

Lying between the optic lobes, the lateral lobes of the cerebellum and the anterior pair of eminences termed 'tuberculum

[21] See Johnston, J. B. The brain of Acipenser. Zool. Jahrb., Bd. 15, 1901, plate 2.

acusticum' is a structure (figs. 5, 6, 8, 15) which at first was provisionally identified as the pineal body and its stalk. In all modern forms, however, the epiphysial stalk is directed upward and forward from the diencephalon, not backward, as in these specimens. In some living elasmobranchs there is a dorso-medial vein in approximately this position,[22] though nothing has been described which resembles this structure exactly. In the specimen of the Mississippian Rhadinichthys, the posterior part of the midbrain roof has been shattered; but at the anterior end there are two small ridges (fig. 4) which resemble the dorsal veins in some of the species of elasmobranchs figured in the work of Rex cited above. It is probable that these ridges in all of our specimens are dorsal veins, and that the enlargement marked * in figure 15 is, in reality, a venous sinus.

The structure labeled 'thalamus' (figs. 4, 5, 6, 9, 17) is situated anteriorly between the optic lobes and the cerebral hemispheres (olfactory lobes). It is single and median, with its upper surface partially abraded in the specimen figured. The full form is ascertained from a study of its mold in other nodules. Posteriorly and between the thalamus and the optic lobe there may be seen a small structure designated on figure 17 'oculomotor nerve;' this may, however, be a blood vessel. Its peripheral relations cannot be determined. Anterior to it and lying in the lower part of the thalamus are four small but distinct elevations, which doubtless represent nuclei of uncertain function.

The hypothalamus (lobus inferior) is very large, as in most recent fishes. It occupies the typical position below and behind the thalamus and below the optic lobes. An eminence at its caudo-ventral angle is probably the hypophysis.

The cerebral hemispheres (marked 'olfactory lobes' on the figures) are small as compared with those of living fishes, although they are distinctly ganoidean in form. The region in front of the expanded olfactory lobes tapers forward slightly into a hollow stalk (figs. 7 and 15), whose cavity is the rhinocoele. If the olfactory bulbs lie farther forward, as in many

[22] Rex, H. Beiträge zur Morphologie der Hirnvenen der Elasmobranchier. Morph. Jahrb., Bd. 17. 1891, p. 417.

teleosts,[23] then this region contains the 'olfactory tracts,' or crura olfactoria. The small size of the olfactory lobe suggests that the olfactory organs were not highly developed; it is, therefore, not improbable that the region designated 'olfactory tract' is really the slender olfactory bulb. This region is, unfortunately, only partially preserved in all the specimens studied, but the portion preserved is very interesting. Doubtless just anterior to the broken end (fig. 15) the tracts separated into the olfactory nerves, as in Rhadinichthys (fig. 4). A cross section of the olfactory bulbs (or tracts) is readily obtained and the structure involved is shown in figure 7. The cavity of the rhinocoele is preserved by the formation of crystals around it. Its form and the fact that the surrounding wall is massive on all sides suggest that at the site of the section we are dealing with olfactory bulb rather than with olfactory crus. The cross section shows that the two bulbs are apparently fused in the medial plane, as in the frog; but it is impossible to determine whether this appearance is artificial or an expression of a real anatomical fusion.

The larger brains of a fish from the Coal Measures are so distinct in some features as to be worthy of special consideration. One of them is figured in lateral view (fig. 9). The chief points of interest are readily observed from an examination of this figure. The olfactory tracts are quite similar in the two types of brains. It will be seen that the olfactory lobes and the thalamus are much smaller in proportion to the size of the brain than in the brains shown in figures 15 and 16. The optic lobes, on the other hand are very much larger and constitute by far the greater part of the brain. There is no median sulcus dividing the lobes as in the smaller brains. Its place is taken by a well marked ridge. There is thus no sure indication of that organ which is tentatively determined as the dorsal blood vessel, though possibly the ridge is formed by the meninges enclosing such a vessel and strongly compressed laterally. The lateral lobes of the cerebellum are very slightly developed and their median ends are not nearly so approximate as in the smaller brains and espe-

[23] In the carp, for instance; see Sheldon, R. E. Jour. Comp. Neur., vol. 22 1912, p. 257, fig. 1 and p. 265, fig. 23.

cially in the brain of Rhadinichthys. The remainder of the posterior portion of the brain is obscured on the two or three specimens which are available for study. The hypothalamus does not differ essentially from that of the smaller brains.

VII. THE ANATOMY OF THE EAR OF THE COAL MEASURES FISH

On either side of the posterior portion of the brain of several specimens of both the Coal Measures and Mississippian fishes there occur the vertical semicircular canals as tortuous vessels which are strongly bent inward in the region of the tuberculum acusticum (figs. 10 and 15). In size the canals seem a little large but this may be due to the increase owing to the segregation and crystallization of the mineral substance composing the fossil. This structure has been fully described by Doctor Parker ('08) in the Mississippian fish and his discussion is referred to on a previous page.

The ear is very completely preserved in one specimen (fig. 10) and the parts of the ear in other specimens are sufficiently well preserved so that it has been possible to reconstruct the complete, or at least approximately complete, anatomy of the semicircular canals in their relationship to each other (fig. 11). The inner ear is well represented in figures 15 and 16, where may be seen the sacculus, the utriculus, and the horizontal semicircular canal with its ampulla, which is rather extraordinary in the enormous expansion of its anterior parts.

The ear as a whole is very unusual and is totally unlike anything I have seen figured in the literature. The chief differences being the unusually enlarged portions of the ampullae. In its general configuration the relation of the canals to each other is about as figured for other fishes, notably Acipenser as figured by Retzius. The *horizontal semicircular canal* is well shown in figures 4, 15 and 16 and needs no further description. The form of this canal is quite constant and I have seen it in six different specimens. The *ampulla* of this canal is very unusual and a portion of it, which has become unusually enlarged, has been labeled *sinus* (fig. 16), with no thought that this has anything

to do with its connection to the sacculus. The upper part of the left vertical semicircular canals is evident in figures 4 and 15. Their connection with the utriculus through the sinus utriculi superior is evident in one specimen (fig. 10) in an undisturbed relation, which has been used as a basis for this portion in the reconstruction (fig. 11). One specimen of a larger brain than that shown in figures 15 and 16 shows the horizontal canals in position on both sides, with portions of their ampullae. The shape of the anterior ampulla (fig. 10, *a.a.*, *s.u.a.*) is sufficiently evident from the drawing. The peculiar enlargement is not confined to one specimen, but is determined in all the nodules examined, including some from another locality (Baldwin, Kansas).

The *sacculus* is evident below the semicircular canal but it is in such a position that it cannot be shown in lateral view of the specimen. Its form is bowl-shaped and it is not possible to delimit it from the utriculus, as is shown in the reconstruction (fig. 11). The *utriculus* is well shown in the various figures (figs. 10, 11, 15, 16). It joins the vertical semicircular canals in an oval sinus utriculi superior.

VIII. THE DURAL CASTS OF THE BRAIN AND SACRAL INTUMESENCE OF THE DINOSAURS

We owe to Professor Marsh ('74–'96) much of our knowledge of the neural anatomy of those gigantic reptiles, the dinosaurs, which witnessed the widespread development of this class and saw the extinction of most of its members. They themselves became extinct in the late Cretaceous or early Tertiary at the onset of mammals, but before becoming lost to the world they attained structural adaptations which will ever be the marvel of the paleontological world.

Since Marsh there have been other workers on dinosaurian neurology. Hay ('09) has discussed the dural cast of a member of the gigantic horned dinosaurs which is carried further by Lull (Hatcher, Marsh, Lull, '07). Osborn ('12) and Brown ('14) have recently given the best accounts of the anatomy of the dino-

saurian brain. Osborn is the first one to call careful attention to the fact that the so-called 'brain casts of dinosaurs' are in reality dural casts and as such do not show the anatomy of the brain, since in all probability the brain did not fill the dural cavity. He based this conclusion on the observations made by Dendy on the brain of Sphenodon.[24] Professor Osborn has very carefully figured the dural casts of the brain cavity of two of the largest dinosaurs, one a herbivore, Diplodocus, a member of the Sauropoda; the other a carnivore, Tyrannosaurus (figs. 18, 19). Both had very large hind limbs, but the skulls in the two are disproportionate, being very large in Tyrannosaurus and insignificant when compared to the size of the body in Diplodocus. If we may imagine a mass of flesh and bones of nearly forty tons in weight being guided by a head the size of that of a horse, this head containing a brain only a fraction the size of the equine animal's, we have a mental picture of Diplodocus (fig. 12). We could not expect much cephalic development of the nervous system, and we find but little. Professor Osborn has kindly permitted me to copy three of his figures and a glance at the brain of Diplodocus is very instructive (fig. 18). Additional interpretations have been made on the figure. The hind limbs of Diplodocus were very large, attaining a standing height of twelve to fifteen feet and the tail was long and heavy. We should expect to find a corresponding sacral intumesence lodging a 'lumbar brain,' nor are we disappointed. Professor Marsh ('81) created considerable interest in the scientific world by announcing that the 'lumbar brain' of Stegosaurus was ten times the size of the cephalic brain. It is certain that the dural cavity of the sacrum has ten times the capacity of the cephalic dural space (Lull, 1910; Amer. Journ. Sci., vol. 30, pp. 361–377).

There is, of course, no assurance that the nervous portion of the sacral intumesence filled the dural cavity. Doctor Williston, who worked out the material of Stegosaurus on which Marsh's original observations were made, tells me that the enlargement was largely confined to the sacrum and was not a tapering in-

[24] Dendy, A. 1911. Phil. Trans. Roy. Soc. London, Series B, vol. 201, p. 227–331.

tumesence as in other animals. Streeter[25] working on the ostrich, has described and figured the 'lumbar brain' in detail and comparatively with the brain and spinal cord. The spinal cord in this large bird does not fill the dural cavity of the vertebrae, nor does the lumbo-sacral intumesence have more than half the diameter of the brain. It is probable that in the dinosaurs the dura mater was the periosteum of the spinal canal. It is also probable, as in the ostrich, that there was a large space between the walls of the canal and the cord filled with arachnoid. There is, however, this difference: the head of the ostrich is proportionately larger than in the dinosaurs (Diplodocus) under consideration. In birds the brain more nearly fills the brain case than in the reptiles, and it has a larger development. While it may not be precisely true that the 'lumbar brain' in the sauropodous dinosaurs was *ten times* the size of the cephalic brain, yet every feature in their anatomy points to the conclusion that it was several times larger; a truly anomalous condition where the greatest mass of nervous tissue is located in the sacral region (fig. 12).

Brown ('14) has recently published some most interesting figures of brain casts and apparently complete inner ears of a new type of dinosaur. While it is to be regretted that Brown has not given us a more detailed study of these sensory structures, yet it is interesting to note the enormous possibilities offered by fossil material for the elucidation of anatomical features. When paleontologists have worked over all of the taxonomic possibilities of fossil vertebrates it is to be hoped that some will turn their attention to the description of anatomical structures as they occur in these fossil vertebrates.

IX. THE BRAIN AND EAR OF A PTERODACTYL

Newton ('88) has given a careful account of the brain cast of a flying reptile, Scaphognathus, one of the Liassic pterodactyls. This cast is apparently a much more accurate copy of the brain than is the case in brain casts of other reptiles, the dinosaurs for instance. It has been thought worth while in this review to

[25] Streeter. Amer. Jour. Anat., vol. 3, no. 1, pp. 1–27, figs. 2–6.

copy Newton's figures of the brain, as he has shown it in lateral and dorsal views. An examination of these figures (fig. 13) will show at once how bird-like the brain of the pterodactyls was. This is, however, no indication of direct avian relationship, but is rather a development in response to the volant habits and to the highly organized condition of the optic apparatus, for the eyes were enormous.

An avian relationship for the pterodactyls has been advocated by several students of these vertebrates, as is indicated, for instance, in the term Ornithosauria, one of the earlier terms under which the pterodactyls were known. This relationship has, however, been largely disproven, and it is now the opinion of the majority of those most competent of expressing an opinion that the pterodactyls were true reptiles, curiously modified for life in the air. They reached the highest volant adaptation of any known animal, not even excepting some of the modern tropical butterflies. An evidence of this high degree of adaptation is given by Williston[26] in the following words: "Notwithstanding the enormous expanse (more than 19 feet) of the wings, these animals when alive must have weighed but little. I doubt very much if one of the largest species reached twenty pounds."

The *optic lobes* in Scaphognathus are as well developed as in some modern birds and much better developed than among the contemporary reptiles, the dinosaurs.

The brain lay very close to the occipital condyle and far behind the orbit (Newton, '88, pl. 77, fig. 1) and between and under the cancellous parietals. The length of the brain from the edge of the occipital foramen to the front of the cerebral lobes is 25 mm.; its greatest width across the optic lobes is 17 mm. The length of the skull was 140 mm.

The large piriform *flocculus* was flattened from above downwards and is attached at its broad end to the side of the hind brain just below the cerebellum.

Portions of three canals of the ear are evident, and there are also indications of the ampullae. There seems to be an aperture

[26] Williston, S. W. 1897. Kans. Univ. Quart., vol. 6, p. 38.

in a deep hollow just in front of the lower part of the paroccipital process, representing the fenestra ovalis auris. In the slenderness of the semicircular canals the remains of these organs in Scaphognathus resemble the goose, Anser domesticus, as figured by Retzius.

X. THE BRAIN CASTS OF THE TERTIARY MAMMALS

Brain casts of mammals have long been known and widely commented on. Gervais ('69), Marsh ('74), Bruce ('83), Scott ('98 and '13), Smith ('03), Osborn ('10), Palmer ('13) and many others have commented on various features of the brain casts of Tertiary mammals. All have noted the major features, such as the large size of the cerebellum and the apparently smooth cerebrum. Scott ('98) has called attention to the fact that the brain casts are dural casts and as such do not exactly copy the cerebral convolutions. Smith ('03) and Palmer ('13) are the first to make an attempt at any neurological study of the brain of these interesting vertebrates. Palmer's paper is the latest contribution to the paleoneurology of the mammalian brain; and he has given the most careful account which has yet been offered. The subject has been touched only in its general features, and much certainly remains to be done (fig. 14). A brief review of the work which has so far been published on mammalian fossil brains will be found in the annotated bibliography.

XI. SUMMARY

The earliest vertebrate-like animals, the Ostracoderms, have preserved external sensory structures, such as sensory canals, lateral eyes, a pineal opening and the opening of the endolymphatic duct.

The brains of the fishes of the Mississippian and Coal Measures are very similar, being identical in a few details. Both types are characterized by very large optic lobes, which in the Coal Measures fish was due to the enormous eye. Nearly all parts of the Coal Measures brain are known, including some of the smaller nerves. The inner ear of one specimen is nearly

completely preserved. The brain and ear are wholly unlike those of any modern fish and no attempt is made at a direct comparison. There are several unusual features about the Paleozoic brains, such as a single, median vagal lobe, the widely separated lateral lobes of the cerebellum, the large optic lobes and the curious condition of the olfactory bulb or tract.

Among the dinosaurs all the available evidence points to a 'lumbar brain' which was considerably in excess, in the mass of nervous tissue, of the cephalic brain. By this it is not intended to indicate that sensory functions were largely confined, to the lumbar region.

The brain casts of Tertiary mammals are dural casts, and do not repeat the smaller features of the cerebrum. These objects have been insufficiently studied.

XII. AN ANNOTATED BIBLIOGRAPHY OF PAPERS ON FOSSIL BRAINS AND OTHER SENSORY STRUCTURES

There are many descriptions of fossil brains, especially mammalian, not listed in this place; but the chief papers are given which will serve as a basis for future students.

ANDREWS, C. W. 1897 Note on the cast of the brain cavity of Iguanodon. Ann. Mag. Natl. Hist., 6th Ser., vol. 19, pp. 585–591, pl. xvi, and 1 text figure. See also: Seeley, H. G. 1880. Pop. Sci. Review, vol. 19, p. 48, pl. 2, fig. 2. Andrews gives excellent figures of the brain cast of this dinosaur, comparing it with American dinosaurs, especially Ceratosaurus.

BLACK, D. DAVIDSON 1915 Notes on the endocranial casts of Okapia, Giraffa and Samotherium. Anat. Rec., vol. 9, no. 1, pp. 56–59. A preliminary report on an interesting study of the surface patterns of the brain of three related mammals, one of which is extinct.

BROWN, BARNUM 1914 Brain casts of Anchiceratops and a Trachodont. In "Anchiceratops, a new genus of horned dinosaurs from the Edmonton Cretaceous of Alberta. With discussion of the origin of the ceratopsian crest and the brain casts of Anchiceratops and Trachodon." Bull. Amer. Mus. Natl. Hist., vol. 33, art. 33, pp. 539–548, pls. 35 and 37. Describes excellent brain casts and complete inner ear.

BRUCE, ADAM T. 1883 Observations upon the brain casts of Tertiary mammals. Contribution from the E. M. Mus. Geol. and Arch. Princeton Coll. Bull. no. 3, pp. 36–45, with pl. 7. Discusses formation of brain casts. Figures and describes very carefully the brain casts of six genera of Tertiary mammals. His conclusions are worthy of note.

BURCKHARDT, R. 1892 Das Gehirn von Triceratops flabellatus Marsh. Neues Jahrbuch f. Mineral., Bd. 2, pp. 71–72, 1 fig. Discusses paper by Marsh (Amer. Journ. Sci., vol. 39, p. 419) and copies figure.

CASE, E. C. 1897 Foramina perforating the cranial region of a Permian reptile and on a cast of its brain cavity. Amer. Journ. Sci. (4), vol. 3, pp. 321–326, with 4 figs. in text. The hypophysis is the most interesting feature of the brain; it descends into the body of the basioccipital. Brain cast preserves only posterior part of brain.

1914 On the structure of the inner ear of two primitive reptiles. Biol. Bull., vol. 27, no. 4, pp. 213–215, with figures. Discusses and figures the inner ear of Edaphosaurus from the Permian and reviews Cope's work (Cope '86) on the ear of another Permian reptile, Diadectes.

COPE, E. D. 1877 a On the brain of Coryphodon. Proc. Amer. Phil. Soc., vol. 16, pp. 616–620, pls. 1–2. Compares brain of Coryphodon, an early ungulate, with the cast of the brain of Arctocyon described by Gervais from France ('72).

1877 b On the brain of Procamelus occidentalis. Proc. Amer. Phil. Soc., vol. 17, pp. 49–52, pl. 1. Brain is figured in three views and is regarded as displaying characters of the archaic Ruminantia. Good general description, though no attempt is made at interpretation.

1877 c The lowest mammalian brain. American Naturalist, vol. 11, pp. 312–313. Describes brain of Coryphodon, the description being the same as in 1877 a. The cerebral characters are not clearly defined; possibly indicating that the brain case was considerably larger than the brain.

1886 On the structure of the brain and auditory apparatus of a theromorphous reptile of the Permian epoch. Proc. Amer. Assn. Adv. Sci., 34th meeting, Ann Arbor, 1885, pp. 336–341: same in Proc. Amer. Phil. Soc., 1885, p. 234; see also Case, 1914.

1888 The pineal eye in extinct vertebrates. Amer. Naturalist, vol. 22, pp. 914–917, pls. 15–18. Discusses and illustrates the occurrence of this organ among fossil vertebrates; figures brain of Diadectes, a Permian reptile; and Belodon, a Triassic reptile.

DAWSON, J. W. 1878 Acadian geology, 3rd edition; Suppl., p. 101. Refers to crystalline lens of eye of fossil fish.

DEAN, BASHFORD 1907 Notes on acanthodian sharks. Amer. Jour. Anat., vol. 7, p. 218. Describes the inner ear and notes the occurrence of lateral line organs preserved in selachians in the British Museum described by Dr. Woodward: Proc. Zool. Soc. London, 1888, p. 126.

1891 Pineal organ in fishes. 19th Rept. Com. Fish, N. Y., p. 307, pls. 1–14.

EASTMAN, CHARLES R. 1908 Brain of Rhadinichthys deani Eastman. In "Devonian fishes of Iowa." Iowa. Geol. Survey, vol. 18, pp. 266–272, text figure 40; pl. 13, figs. 8–9. Describes nearly complete brain of an early ganoid, with nerves, inner ear and arteries. The illustrations are not suited to a detailed study of the brain characters.

GAUDRY, ALBERT 1896 Progrès de l'intelligence. In "Essai de paléontologie philosophique." Chapter VII, pp. 139–154, with 14 figures of brains

of various fossil vertebrates. Reviews the work done on fossil brains and points out their significance in the development of intelligence.

Gervais, Paul 1869 Memoires sur les formes cerebrales propres aux edentes vivants et fossiles. Nouvelles Archives du Museum d'Histoire Naturelle de Paris, tome 5, (ser. 1), pp. 1–56, pls. 1–5. Figures in beautiful plates brain casts of Megatherium, Mylodon, Scelidotherium, but no attempt is made to analyze the various parts. Comparisons made with recent edentates. Many footnote references. A splendid memoir for students of paleoneurology.

1872 Forme cérébrale de Cephalogale Geoffroyi. Journal de Zoologie, vol. 1, pp. 132–134, pl. 6. Figures and briefly discusses an excellent dural cast of a carnivore.

Gregory, W. K. 1914 The dawn man of Piltdown, England. American Museum Journal, vol. 14, p. 196, fig. 8. Figures dural cast of Eoanthropus dawsoni, from the Pleistocene.

Hatcher, Marsh, Lull 1907 The brain and brain cavity of Ceratopsia. In "The Ceratopsia," Monograph XLIV, U. S. Geol. Survey, p. 36, figs. 31–34. The size of the brain in this group of dinosaurs, as indicated by a study of the dural casts is smaller in proportion to the size of the body than in any other known group of vertebrates.

Hay, Oliver P. 1909 On the skull and the brain of Triceratops, with notes on the brain-case of Iguanodon and Megalosaurus. Proc. U. S. Nat'l. Museum, vol. 36, pp. 95–108, pls. 1–3. Describes osteology of the brain case and figures (plate 3) the dural casts of Triceratops, especially noteworthy on account of the large size of the hypophysis.

von Huene, Friedrich 1913 The brain case of Eryops. In "The skull elements of the Permian Tetrapoda." Bull. Amer. Mus. Natl. Hist., vol. 32, p. 320, figs. An unusual skull shows the osteology of the brain case and allows a study of the chief foramina for the exit of the cranial nerves.

Hulke, J. W. 1871 Brain of Iguanodon. Quart. Journ. Geol. Soc., vol. 27, p. 199, pl. Figures a fragment of the skull of a dinosaur, doubtfully Iguanodon, showing part of the brain case with a few nerve foramina.

Lankester, E. Ray 1900 The significance of the increased size of the cerebrum in recent as compared with extinct mammalia. Cinquartenaire Soc. Biol. 8, vol. Jubilaire, pp. 48–51. A few remarks on the gradual increase in size of the cerebrum during the Tertiary.

Marsh, O. C. 1874 Small size of the brain in Tertiary mammals. Amer. Journ. Sci., (3), vol. 7, pp. 66–67. Refers to the importance of the study of brain-casts of fossil mammals in their bearing on the evolution of the Mammalia.

1876 The brain of Dinoceras. Amer. Nat'l, vol. 10, p. 182. Short note with figure, same as 1886.

1877 Brain of Coryphodon. Amer. Nat'l, vol. 11, p. 375.

1878 Brain of a fossil mammal. Nature, vol. 17, p. 340. Same as preceding.

1880 Brain of Hesperornis (Hargeria). In "Odontornithes, a monograph on the extinct toothed birds of North America." Memoirs of the Peabody Museum of Yale College, vol. 1, pp. 8–10, figs. 1–3. Com-

pares brain of this bird with that of recent birds. Brain in extinct form about one-fifth length of the skull, proportionately smaller than in modern birds with larger optic lobes.

1881 Spinal cord, pelvis, and limbs of Stegosaurus. Amer. Journ. Sci., vol. 21, p. 167, pl. 6: Ibid, vol. 19, p. 253, March, 1880. Sacral intumescence has cavity with ten times the capacity of the brain case.

1885 On the size of the brain in extinct animals. Nature, vol. 32, p. 562. States general law of brain development; gradual increase in the size, especially of the cerebrum, of the Tertiary Mammalia. The brain of the large Eocene mammals was very small.

1886 Brain of the Dinocerata. Monograph X, U. S. Geol. Surv., pp. 53–67, figs. 57–83, pl. 6. Discusses the very small brain of these gigantic mammals and compares by figures with other extinct species.

1893 The skull and brain of Claosaurus. Amer. Journ. Sci., vol. 45, Jan., pp. 83–86, pls. 4–5. The brain is elongate, the hypophysis large and in size the brain is very small as compared with the skull.

1896 Brain casts in dinosaurs. In "Dinosaurs of North America," pls. 76–77 and text fig. 34. A résumé of all work previously done on dural casts of American dinosaurs. Figures casts of brain cavity of seven genera of dinosaurs and compares them with the dural cast of the alligator.

von Meyer, Hermann 1865 Fossiles Gehirn von einem Säugethier aus der Nieder-Rheinischer Braunkohle. Paleontographica, Bd. 14, p. 37, pl. 10. Excellent brain cast of a carnivore commented on and beautifully figured, but with no attempt at interpretation.

Moodie, Roy L. 1911 A contribution to the soft anatomy of cretaceous fishes. Kans. Univ. Sci. Bull., vol. 5, no. 15, Bibliography. The chief papers on the soft anatomy of fossil vertebrates are noted in the bibliography.

Newton, E. T. 1888 On the skull, brain and auditory organ of a new species of pterosaurian (Scaphognathus purdoni) from the Upper Lias near Whitby, Yorkshire. Phil. Trans. Roy. Soc. London, vol. 179 (B), p. 503, pls.; same in: Proc. Royal Soc. London, vol. 43, p. 436. Sides of brain case ossified but open in front, brain very small, large optic lobe and well-preserved flocculus with a portion of the semicircular canals of the ear. Cerebrum large and smooth, bird-like; olfactory stalk small. Brain compared by figures with brains of Cretaceous bird, lizard, and recent bird.

Osborn, H. F. 1910 Brain casts. In "Age of mammals," p. 173. Figures brain proportions in archaic and modern mammals.

1912 Crania of Tyrannosaurus and Allosaurus. Mem. Amer. Mus. Natl. Hist., N. S., Vol. I, Pt. II, p. 21, pls. 3–4, fig. 17. Figures dural casts of Tyrannosaurus and Diplodocus, and discusses nature of dural casts. The most careful account of dinosaur brain casts which has yet appeared.

Palmer, R. W. 1913 The brain and brain-case of a fossil ungulate of the genus Anoplotherium. Proc. Zool. Soc. London, Pt. IV, pp. 878–893, with 8 figures. A very careful study of the brain and brain-case of an early Eocene ungulate which is of interest in that the cerebellun is very large and the cerebral convolutions well marked.

Parker, G. H. 1908 Special description of the auditory organ and other soft parts. In "Devonian fishes of Iowa." Iowa Geol. Survey, vol. 18, p. 272. Confirms results of Eastman ('08).

Patten, William 1912 Olfactory and auditory organs (in Ostracoderms). In "Evolution of the vertebrates and their kin," p. 356. Describes and figures all evidences of sensory structures among the Ostracoderms.

Pouchet, Georges 1868 Memoire sur l'encephale des Edentes. Journal de l'Anatomie et de la Physiologie, tome 5, 6. Discusses cranial casts of Mylodon and Glyptodon.

Reiss, Otto M. 1895 Ueber Phosphoritisirung der Cutis, der Testikel und des Rückenmarks bei fossilen Fischen. Archiv f. mikros. Anatomie, Bd. 44, pp. 87–119, mit Tafel 6. See also Bd. 52, by same author on petrifaction of muscle: Ibid, Bd. 41, p. 492; 1898, p. 262.

Scott, W. B. 1898 Brain of Cynodictis. In "Notes on the Canidae of the White River Oligocene." Trans. Amer. Philos. Soc., vol. 19, pp. 374–375, pl. 19, fig. 12. The brain of this early canid differs considerably from recent dogs in the large size of the cerebellum which is "simpler than in the recent dogs." Scott observes in regard to the nature of casts: "It should not be forgotten that the brain-cast very probably fails to reproduce all of the fissures."

1913 Brain casts. In "History of the land mammals in the western hemisphere," p. 41. Refers to the importance of the study of brain casts.

Seeley, H. G. 1901 The brain in pterodactyls. In "Dragons of the air," pp. 54–56, fig. 19. Appletons, London. Reviews the specimens which show evidences of brain structures.

Smith, G. Elliot 1899 The brain in the Edentata. Trans. Linn. Soc. Lond., (Zool.), vol. 7, pp. 277–394, with 36 figs. The brain of the glyptodonts, and Megatherium are referred to in comparison with the brains of recent Edentates.

1903 The brain of the Archaeoceti. Jour. Comp. Neur., vol. 13, no. 1, pp. 41–52, with figs. The brain of Zeuglodon is studied from two casts derived from the Eocene deposits of Egypt. This brain is compared with that of a Monodon fetus and Cogia greyi. The brain of the zeuglodonts, in common with other early mammals, shows a strong development of the cerebellum, with apparently smooth cerebrum.

Wiedersheim, Robert 1878 Ueber Labyrinthodon rütimeyeri. Ein Beitrag zur Anatomie von Gesammtskelet und Gehirn der triassischen Labyrinthodonten. Abhandl. d. schweiz. paleontolog. Gesellschaft, Bd. 5, pp. 1–56, mit 3 tafln. The supposed brain cast of this triassic labyrinthodont is very dubious. If a cast of a cavity at all, it is that of the cranial cavity and not of the immediate brain-case. The size of the cast is out of all proportion to the size of the skull. The results of the paper are open to grave question.

von Zittel, Karl 1887 Handbuch der Paleontologie. Bd. 3, Abth. 1, p. 746. Refers to brain and sacral casts of dinosaurs.

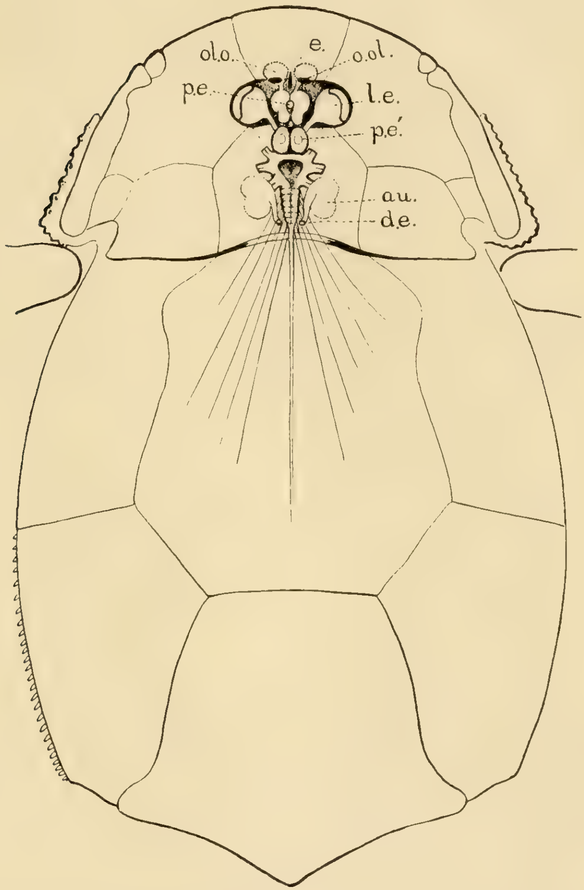


Fig. 1 Outline of the cephalic region of Bothriolepis. Seen from the neural surface, showing the probable size and location of the brain and principal sense organs. The occular plates are not shown. × 1. Drawn by Professor Patten.

au., membranous labyrinth
d.e., ductus endolymphaticus
e., vertical ethmoidal plate
l.e., lateral eyes
o.ol., opening to olfactory organs
ol.o., olfactory organs
p.e., unpaired parietal eye
p.e'., paired parietal organs
b.pl., membranous or cartilage plate forming the floor of the endocranium

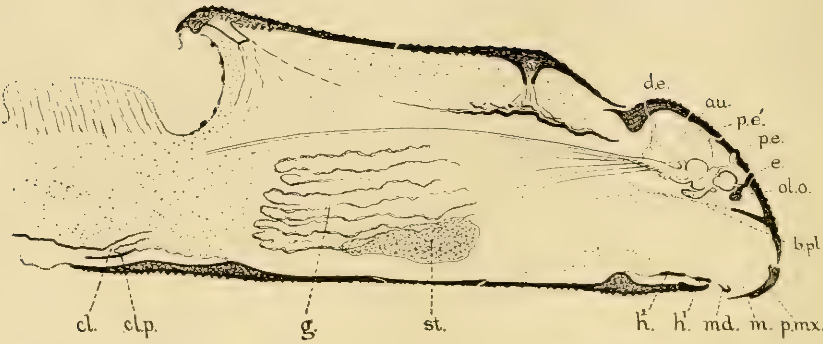
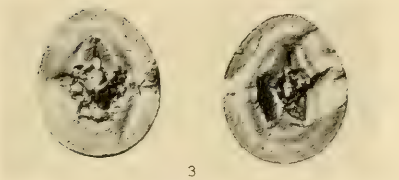


Fig. 2 Sagittal section of the cephalic region of Bothriolepis. × 1. Drawn by Professor Patten.

cl., cloacal opening
cl.p., oval bony plate over-lapping the cloacal opening
g., gills
h[1].*h*[2]., bony plates covering the first and second hyoid arches
m., mouth
md., mandible
p.mx., premaxillae
other letters as in figure 1

Fig. 3 Nodules from the Waverly shales, (Mississippian) of Kentucky, containing the brain and ear of Rhadinichthys deani Eastman. × 1. Courtesy of Doctor Eastman.

Fig. 4 The oldest known fossil vertebrate brain; drawn with the aid of a reading glass from the photograph (fig. 3). Rhadinichthys deani Eastman, a Mississippian ganoid, a member of the family Paleoniscidae, related to the modern sturgeons. The posterior part of the brain has been broken away. At the anterior tip of the olfactory tract is seen an enlargement which may be the olfactory sac. Just posterior to the thalamus are two diverging ridges which doubtless represent venous blood vessels. × 10. The original photograph (fig. 3) from which figure 4 is made shows under a lens all of the detail which is shown in figure 4, with perfect distinctness, though this detail is not visible in the half tone reproduction.



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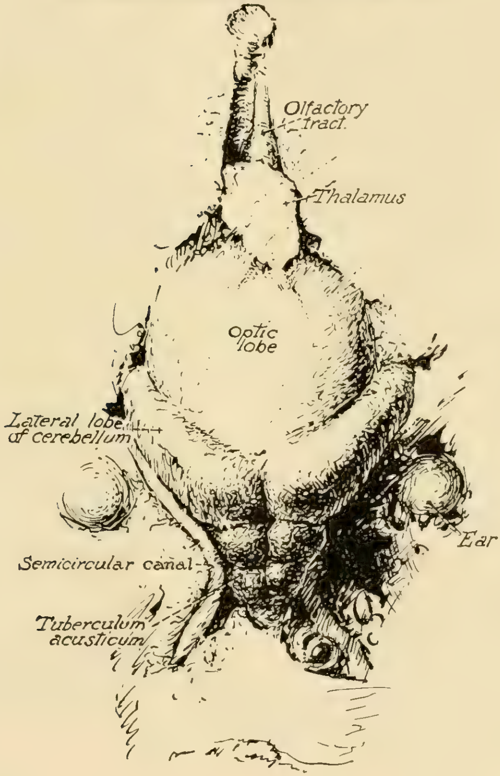
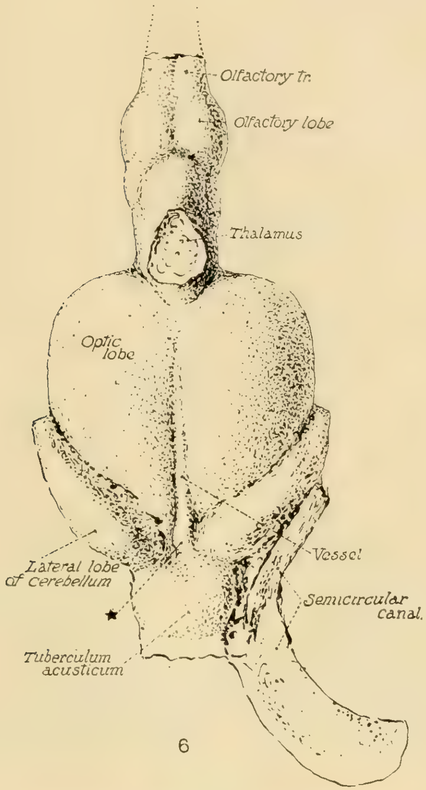

Olfactory tract
Thalamus
Optic lobe
Lateral lobe of cerebellum
Ear
Semicircular canal
Tuberculum acusticum

4

Fig. 5 A fish brain from the Coal Measures of Kansas, before preparation, as it appeared after the containing nodule had been fractured. Intended to show the manner of preservation. This is the brain figured in dorsal view in figure 6 and in lateral view in figure 17. The encrusting matrix was worked away with a needle while the object was under a binocular. The skull bones and cartilage had disintegrated and become transformed into a soft phosphate. × 10.



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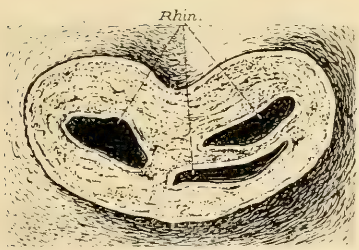

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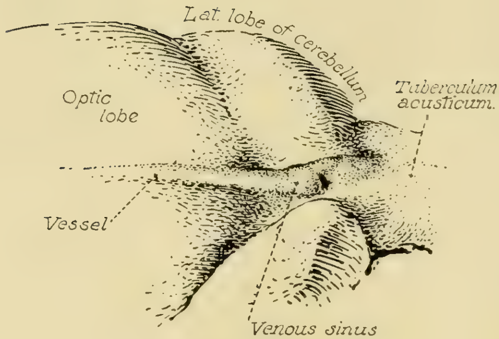
Fig. 6 Dorsal view of the brain of a Coal Measure fish. × 5.5. This same brain is figured in figures 5 and 17. The type of brain is entirely similar to the one shown in figures 15 and 16. (*) marks a venous sinus, formerly interpreted as pineal body. For discussion of these points see text.

Fig. 7 The cross section of the olfactory tract of the Coal Measures fish brain shown in figures 15 and 16. × 40. *Rhin.*, rhinocele.



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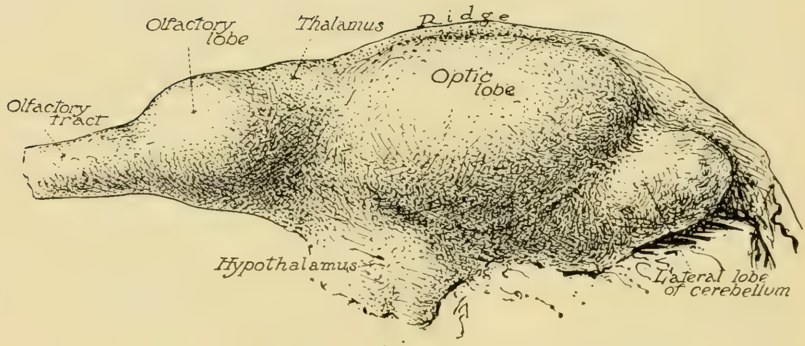

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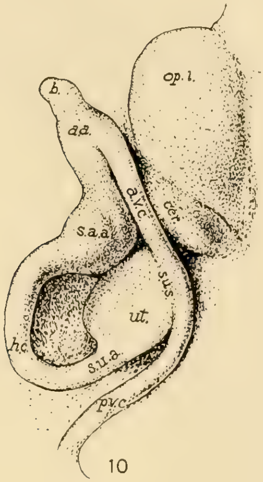
Fig. 8 Postero-lateral view of the intercerebellar region of the brain of the Coal Measures fish shown in a figures 15 and 16, to shows details of the supposed dorsal blood vessel. The posterior enlargement is possibly a venous sinus, although it was first interpreted as a pineal body. The objections to its being a pineal organ are that its position is most unusual and its stalk is directed in the opposite direction to that which the stalk usually occupies. It corresponds very well with a venous vessel as figured and described by Rex. × 8.

Fig. 9 Left lateral view of one of the larger brains of a Coal Measures fish from Kansas. Compare with figure 16, from one of the smaller brains. The general plan of the two brains is similar. × 7.



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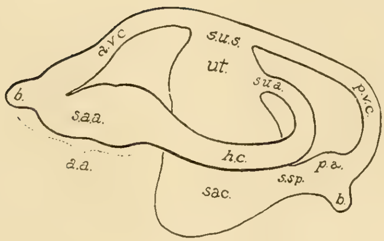

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Fig. 10 Drawing of the left inner ear of a fish from the Coal Measures of Kansas. × 7. *a.a.*, anterior ampulla; *a.v.c.*, anterior vertical semicircular canal; *b.*, ampullary enlargement; *cer.*, lateral lobe of the cerebellum; *h.c.*, horizontal (lateral) semicircular canal; *op.l.*, optic lobe; *p.c.v.*, posterior vertical semicircular canal; *s.a.a.*, an accessory enlargement of the anterior ampulla; *s.u.s.*, sinus utriculi superior; *ut.*, utriculus; *s.u.a.*, sinus utriculi anterior; this sinus enters the utriculus in a postero-lateral direction.

Fig. 11 A reconstruction of the inner ear of a fish from the Coal Measures of Kansas; based on three specimens. × 7. *a.a.*, anterior ampulla; *a.v.c.*, anterior vertical semicircular canal; *b.*, anterior ampullary enlargement. (In two specimens this enlargement is three times the size here represented); *h.c.*, horizontal (lateral) semicircular canal; *p.a.*, posterior ampulla; *p.v.c.*, posterior vertical semicircular canal; *s.a.a.*, an enlargement of the anterior ampulla; *sac.*, sacculus; *s.s.p.*, sinus sacculi posterior; *s.u.a.*, sinus utriculi anterior; *s.u.s.*, sinus utriculi superior; *ut.*, utriculus.

Fig. 12 Relative size of the brain and spinal cord of a dinosaur. $\times 1/140$. The reconstruction is based on outline figures of the body after Matthew and is in the main that of Brontosaurus. Osborn's figures of the vertebrae of Diplodocus, Riggs' figures of the vertebral column of Apatosaurus, Marsh's figures and discussion of the brain and sacral casts of Stegosaurus have all been studied in making this figure.

It represents only an approximation to the truth. The heavy line running through the body is the brain and spinal cord. It represents the dural cast of the vertebral and cephalic spaces and, since we know that in Sphenodon the brain occupied only about one-half of the space and that in the lizard (Leche, Der Mensch, p. 206) a similar condition obtains, we may assume that the brain and spinal cord of the dinosaurs occupied only a fraction of the space. Even allowing a larger fraction for the head than we do for the lumbar region, the 'lumbar brain' would be still many times larger than the cephalic brain.

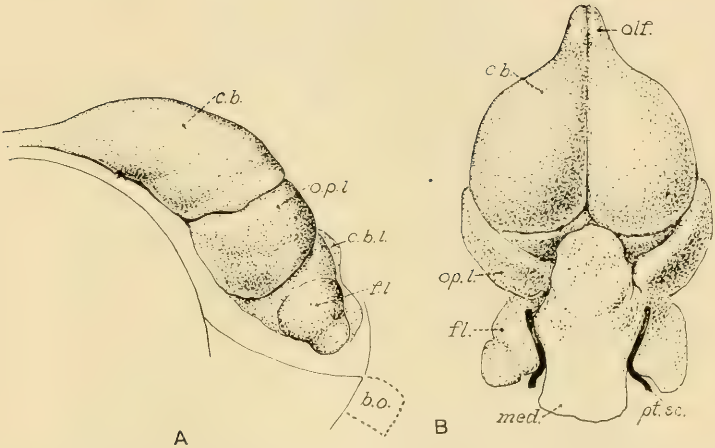
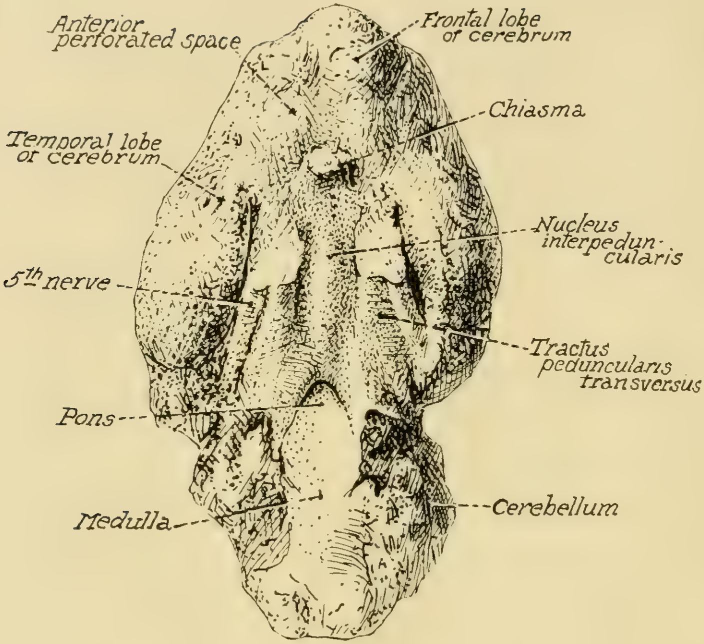


Fig. 13 A Brain cast of the Liassic Pterodactyl, Scaphognathus purdoni, seen from the left side. × 1.5. After Newton ('88, pl. 78, fig. 6). *cb.*, cerebrum; *op.l.*, optic lobe; *cbl.*, cerebellum; *fl.*, flocculus; *b.o.*, basioccipital.

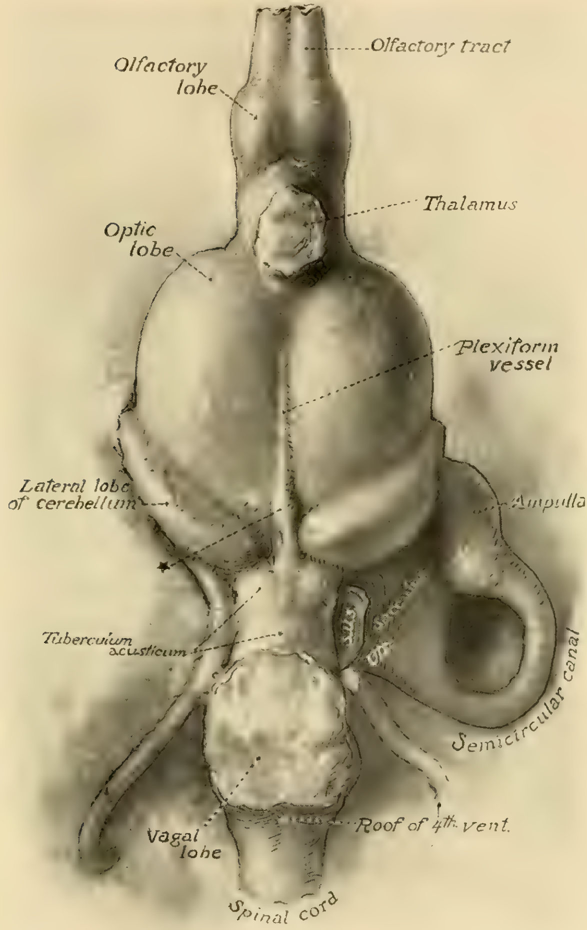
Fig. 13 B Brain cast of same, seen from above and behind. The right side is only partly exposed in the fossil. × 1.5. After Newton ('88, pl. 78, fig. 7). *olf.*, olfactory lobe of brain (including the olfactory tract); *cb.*, cerebrum; *op.l.*, optic lobe; *fl.*, flocculus; *pt.sc.*, posterior vertical semicircular canal; *cbl.*, cerebellum; *med.*, medulla oblongata.



14

Fig. 14 Ventral view of the brain cast of an oreodont mammal, probably Merycoidodon culbertsoni Leidy, from the White River series (Oligocene) of South Dakota. × 1. Scott ('13, p. 372) says of these animals: The Oreodontidae "was one of the most characteristic of North American artiodactyl families, and its members were exceedingly abundant throughout the Upper Eocene, the whole Oligocene and Miocene, ending their long career in the Pliocene. In distribution the family was exclusively North American, and no trace of it has been found in any other continent. . . . . Dr. Leidy, who first discovered and named most of the genera, spoke of them as combining the characters of camel, deer and pig, and called them 'ruminating hogs.' . . . . "

Fig. 15 Dorsal view of the brain and inner ear of the Coal Measures fish from Kansas. × 8. The proportions of the parts of the brain shown in figures 15, 16, and 17 are accurately obtained by measurement with fine pointed calipers under the binocular, adjusted by a fractional millimeter scale. The entire length of the brain, as preserved in the best specimen which is figured in this series is a fraction over 15 mm. The dorsal portions of the thalamus and vagal lobe were broken or eroded before the specimens were studied. The sinus utriculi superior (*s.u.s.*) is evident as a broken end just above the 'S' of the word sacculus. The utriculus (*Utr.*) and sacculus have apparently a wide connection and the limits are uncertain, as indicated in the lettering. They resemble greatly the structures of the same name in Acipenser sturio. From the broken end of the sinus utriculi superior (*s.u.s.*) arose the anterior and posterior vertical semi-



15

circular canals. The structure labeled *ampulla* is the external ampulla of the horizontal semicircular canal, which is the one shown in the figure. The posterior part of the external ampulla is enlarged into a prominent portion which in figure 16 is labeled sinus, with no thought of its being the utricular sinus. The plexiform vessel may be the stalk of the epiphysis or, as is more likely, the median venous blood vessel. The longitudinal tubular vessels to either side of the posterior portions of the brain are the upper parts of the vertical semicircular canals. The structure labeled with a star (*) is what at first was looked upon as a pineal body, but it is more probably a venous sinus.

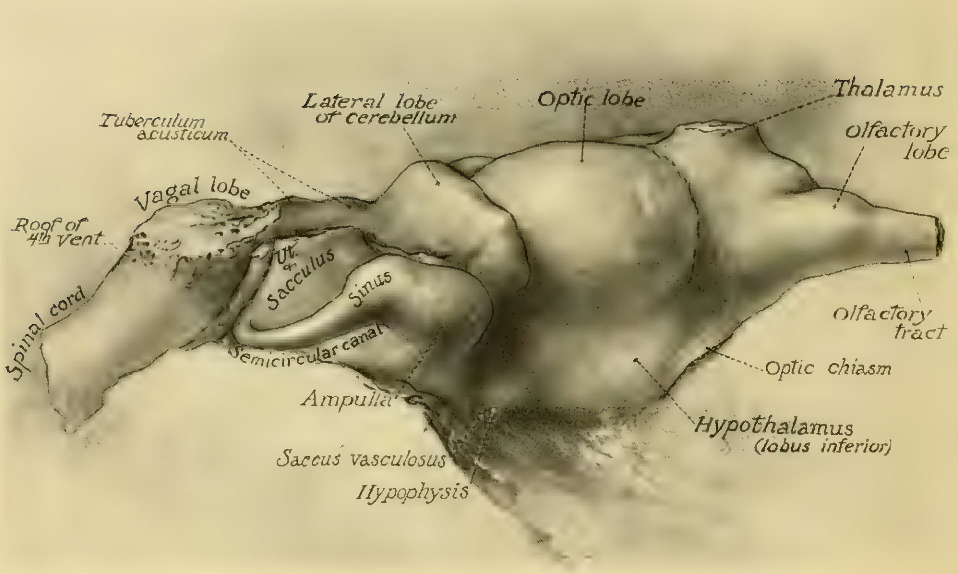


Fig. 16 Right lateral view of the same brain as shown in figure 15. × 8. The portion of the external ampulla labeled *sinus* is very unusual. The anterior ampulla is evident on several other specimens and is described and figured under the section on the ear. The utriculus (*Ut.*) and sacculus are similar to those of Acipenser as figured by Retzius. The upper part is, of course, the utriculus and the lower part the sacculus, which latter is evident below the external (horizontal) semicircular canal.

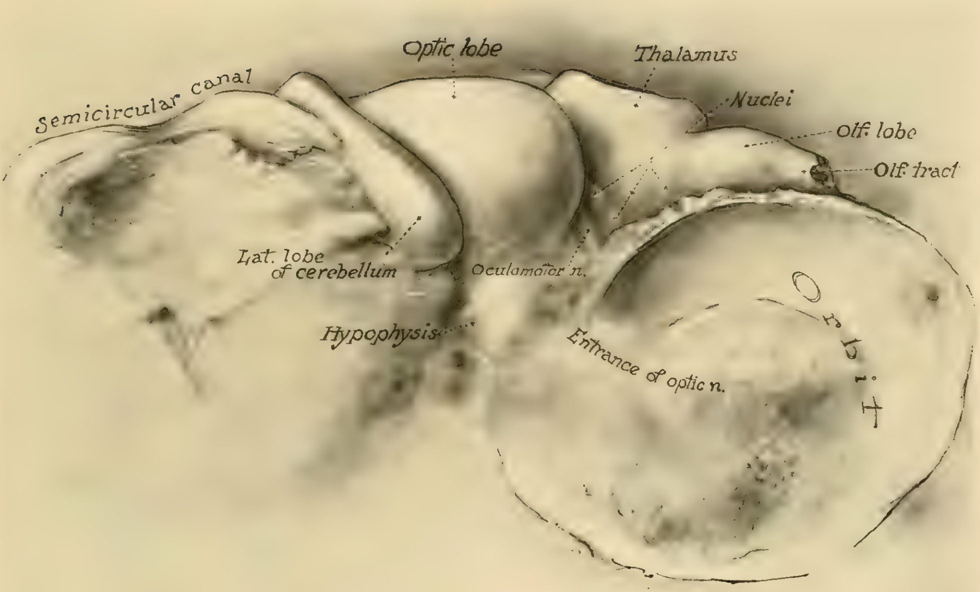


Fig. 17 Right lateral view of a fish brain from the Coal Measures of Kansas, showing especially the size of the orbit and its relations to the various parts of the brain. × 8. The structures labeled nuclei are quite evident on this brain, but are not apparent on the one shown in figure 16.

Fig. 18 (1) Right lateral view of the dural cast of the skull of Tyrannosaurus rex Osborn, from the Upper Cretaceous of Hell Creek, northern Montana. × less than ½. All figures published through the courtesy of Professor H. F. Osborn. (2) Left lateral view of the brain cast of Diplodocus. × less than ½. (3) Lateral view of the right side of the brain case of Diplodocus. × less than ½.

REFERENCE LETTERS (1)

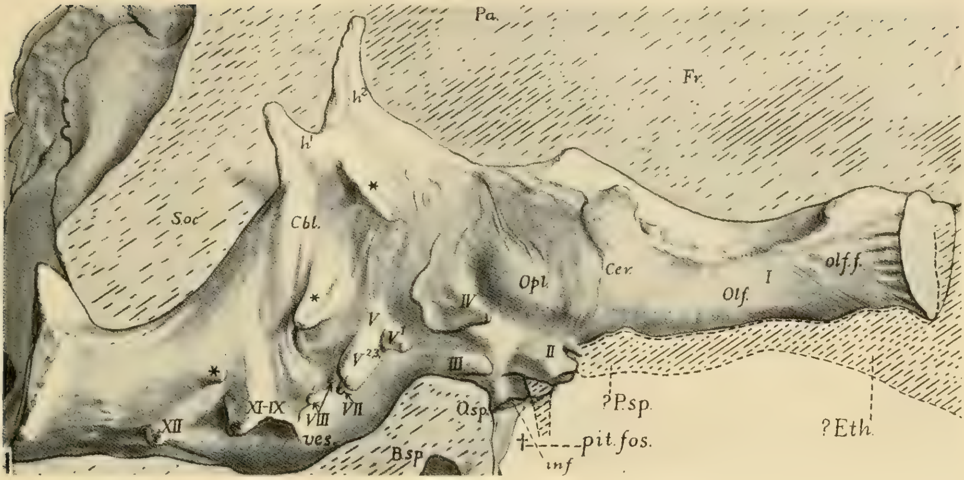
B.sp., basisphenoid
Cbl., cerebellum
Cer., cerebral hemisphere
?Eth., ethmoid
Fr., frontal
h^1, dura mater projection
h^2, dura mater projection
Inf., infundibulum
I, II, III, IV, V, IX–XI, XII, cranial nerve roots
Olf., olfactory tract
Olf.f., olfactory sac.
Op.l., optic lobe
O.sp., orbitosphenoid
Pa., parietal
Pit. fos., pituitary fossa
?P.sp., presphenoid
Soc., supraoccipital
ves., region of vestibulum auris

REFERENCE LETTERS (2)

B.oc., basioccipital
Car.in., point where carotid canal passes into pituitary fossa
ep., epiphysis
for.mag., foramen magnum
Fr., frontal
Inf., infundibulum
O.sp., orbitosphenoid
Pa., parietal
?P.sp., presphenoid
s.end., saccus endolymphaticus
s.oc., supraoccipital
ves., recessus vestibuli auris.
I, II, III, IV, V, VI, IX–XI, XII, cranial nerve roots

REFERENCE LETTERS (3)

B.oc., basioccipital
B.sp., basisphenoid
Car.in., carotid canal
ex.oc., exoccipital
Fr., frontal
f.pin., pineal foramen
O.sp., orbitosphenoid
Pa., parietal
?P.sp., presphenoid
pit.fos., pituitary fossa
pr.ot., prootics
S.en., saccus endolymphaticus
S.oc., supraoccipital
ves., recessus vestibuli auris
I, II, III, IV, V, VI, VII, IX–XI, XII, foramina for exit of the cranial nerves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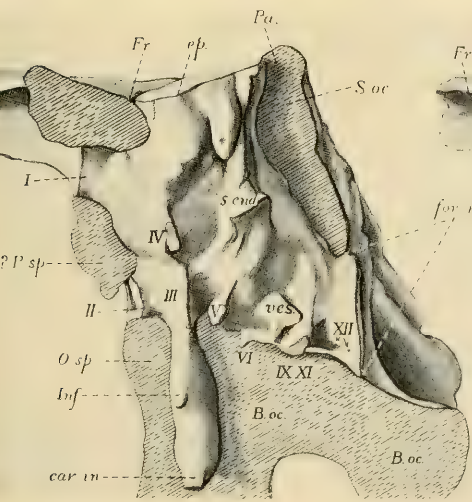
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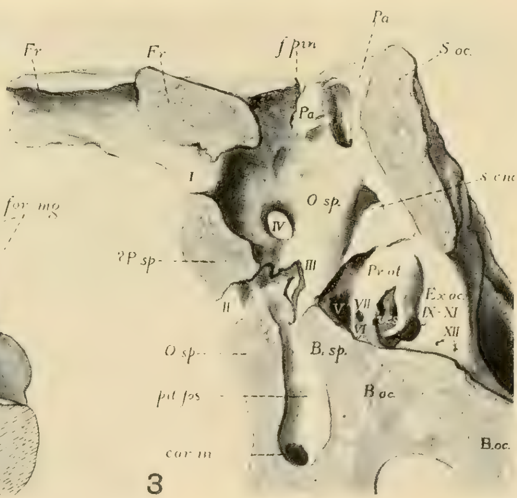
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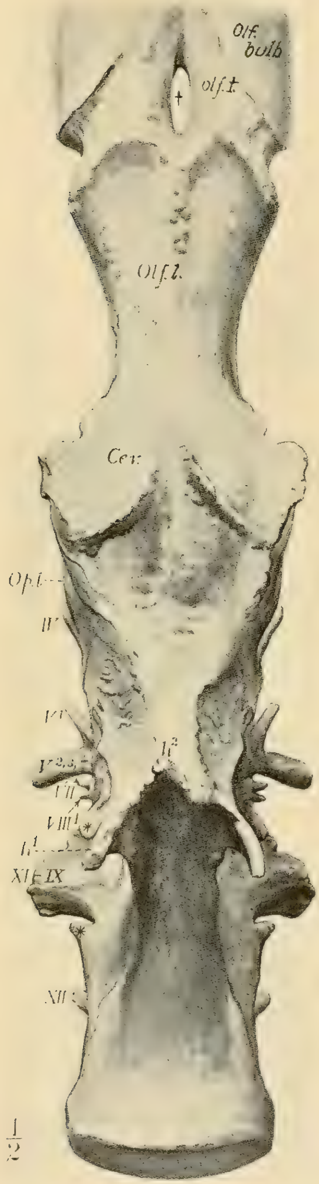
3

Fig. 19 Dorsal view of the brain cast of Tyrannosaurus rex. $\times \frac{1}{2}$. The skull to which this brain belonged was approximately four feet in length. Courtesy of Professor Osborn.

cer., cerebral hemisphere
h^1 *and* h^2, prolongations of dura mater
Olf.bulb., olfactory bulb
Olf.l., olfactory lobe
Olf.t., olfactory tract
Op.l., optic lobe
IV, V, VII, VIII, XI–IX, XII, cranial nerve roots


Olf. bulb
olf.t.
Olf.l.
Cer.
Opt.
IV
VI
h^2
$V^{2,3}$
VII
$VIII^1$
h^1
XI+IX
XII
$\frac{1}{2}$

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A STUDY OF THE AMERICAN NEGRO BRAIN

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SEVEN FIGURES

INTRODUCTION

The work on which this report is based was offered by Mr. Keegan as a graduate thesis, and the detailed description of each brain together with full illustrations is on file in the library of the University of Nebraska.

The material employed consists of thirteen brains, divided into nine adult male brains, three adult female brains and one full time fetal brain (female). The subjects were obtained from the dissecting material in the laboratory. Only those presenting marked negroid features were chosen because we wished as far as possible to eliminate the influence of white blood. The brains were all hardened *in situ* by formaline injection in the carotids, which in the majority of instances furnished satisfactory specimens.

The number of specimens is small, hence no attempt will be made to establish a type of convolution pattern for the Negro; when variation percentages are given it is simply to facilitate comparison with other observations. The report will be confined entirely to the macroscopic study of the brain surface; questions involving nomenclature and methods of interpreting obscure fissure patterns will not be discussed, for these points have been fully considered by one of us in a previous paper (Poynter '12). The work just referred to contains a full literature list, so it will not be necessary to include in the bibliography any titles except those directly referred to in the body of the work.

The term Negro is commonly applied to all dark-skinned peoples when this feature is accompanied with other characters.

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In Huxley's classification the negroid type includes all individuals in which the skin and eyes are brown or black, the hair the same color, short, woolly and scant, the skull dolicocephalic, the forehead rounded, the nasal bones flat and the teeth prominent. Deniker classifies them as follows: "The Negroes may likewise be divided into two sub-races: (a) The Nigritans, of the Sudan and Guinea, more prognathous (more 'negroid,' if we may thus express it) than (b) The Bantus of subequatorial and southern Africa." The remainder of the dark-skinned woolly or curly haired, broad-nosed people he divides into six races; Bushmen, Negrito, Ethiopian, Australian and Dravidian, each placed with a rank equal to that of the Negro as just defined.

The American Negro originally came from the east coast of Guinea and consequently belongs to the Nigritian sub-race as classified by Deniker. Ever since 1785 the Negro has been a conspicuous figure in the history of this country and his place in the racial scale has been much discussed. His inferior social and educational status is generally admitted but the question as to whether this subordinate position is grounded in structural inferiority is doubted, and upon the settlement of this point the solution of the race problem in a large measure still rests.

Proof of the inferior position of the Negro in the racial scale was first sought in structure and it was suggested that he presents morphological features which suggest a closer relation to the lower animal forms than shown by the so-called higher races. However, more extensive study has not proven that these structural differences, when they exist, necessarily indicate inferiority. Boas states, "This is, however, no proof whatever that these differences signify any appreciable inferiority of the Negro * * * * * for these racial differences are much less than the range of variation found in either race considered by itself."

Some attempts have been made to establish racial characteristics in the brain. The first of these had to do with brain weight, and, while there is still some division of opinion on the subject, it may be safely said that no fundamental basis has been established for the determination of race, sex or mental development through gross weight of the brain. The next step was a study

of the convolution pattern with the object of discovering particular features for different races, characters suggesting primitive development or indications of the mental traits. Few comprehensive studies from a racial standpoint have been made, so opinions based on these must be cautiously expressed. It would seem that fissure and convolution variations possess no value as race characters, but it must be remarked that the process of development is still imperfectly understood. When we can interpret growth processes and localize function more exactly, perhaps variations which are now termed individual will take on a racial significance.

No comprehensive study of the Negro brain has as yet been published. Some features have been carefully investigated by Bean, and Cunningham has drawn comparisons from a small series in his Memoir, but most anthropologists have employed generalizations when referring to it. It seems to be generally agreed that the Negro brain is more simply convoluted than the Caucasian, but such a character is too subject to individual variation in both races to establish a standard for race or intelligence.

Bean ('06) has suggested the points of inferiority of the Negro in the following: "The Negro has the lower mental faculties (smell, sight, handcraftsmanship, body sense, melody) well developed, the Caucasian the higher (self control, will power, esthetic sense and reason)." Or, expressed in another way, the Negro is more objective, the Caucasian more subjective. Granting the correctness of this analysis, we may examine the brains of the two races with this idea in view. It is generally agreed that the frontal lobe, and anterior association center, are relatively and actually smaller in the Negro than in the European. Generally associated with this flattened frontal lobe is an unusually prominent inferior parietal area or parietal association center which gives rise to the term 'square cut' occipital contour as an indication of inferiority (Duckworth '07). This does not prove, however, the inferiority of the Negro brain, for we can only assume that the parietal association center is primarily an objective sense center and do not know whether

prominent parietal development is an indication of inferiority or superiority. On the other hand, it might be possible that the depressed frontal lobe and prominent parietal area should be interpreted as race characters being in some way correlated with head shape.

The work of Smith ('04) has done more than that of perhaps any other observer to place brain investigations on a sound scientific foundation, and, while his work is based on a small amount of absolute evidence of the primary relation of sulci and cortical functional areas, the excellent results of its application merit a tentative acceptance of the principle. His work was confined largely to the region of the area striata which definitely localized the cortex. The cause of the change in fissures between ape and man is attributed mainly to the growth of the parietal association center in the human brain.

The difficulty of applying the principle to other regions of the brain is due to the obscurity of morphological or functional areas of the cortex, and this is particularly true of the association centers. Sundry influences are brought to bear on the sulci in their development which cause the disappearance of the original definite relationship to the cortical areas. Smith says: "But when we consider how plastic a material the cerebral cortex is, and how complex are the factors that exert an influence on it during its expansion, the wonder is, not that the coincidence of a sulcus and the boundary line between two areas should not be mathematically exact in every case, but that it should ever occur."

If we have correctly interpreted the results of observations on the fissure and convolution variations, we may conclude that the various lists of Simian or inferior characters which have been published from time to time are at present of doubtful value and that conclusions based on them are unreliable. Dr. Mall ('09) has summed up the matter for the Negro as follows: "With the present crude methods, the statement that the Negro brain approaches the fetal or Simian brain nearer than does the White is entirely unwarranted."

The study of a series of Negro brains in comparison with a series of Caucasian brains should present the most promising field for the establishment of differentiating characters, since the two races are apparently so remotely related. Numerous isolated observations have been made on the Negro brain, but the literature still lacks a detailed presentation of a series of such brains. The following report is offered with the hope of, in a measure, supplying this lack. We have not attempted to establish a group of supposed inferior characters but simply to record the arrangement of the gyri and sulci in a series of brains and as far as possible interpret the growth process in different areas with the resulting influence on the convolution pattern.

DESCRIPTION

In the following description the terminology suggested by Retzius will be used except in the occipital region, which in the Negro brain seems to lend itself better to the more recent usage of Elliot Smith.

The fissura Sylvii propria is remarkable for its very straight course. In the majority of hemispheres there is no pronounced upturning at the posterior end. In all but one hemisphere of the series a terminal bifurcation can be identified, but in a few one ramus is very rudimentary. Three hemispheres represent a communication between the ramus posterior descendens and a contiguous sulcus. Such connection is obliterated in the other brains by the development of a very distinct posterior operculum which can be identified in 92 per cent of the series and appears to be a large factor in the formation of the bifurcation just referred to. Cunningham ('92) has noted a similar condition and Appleton ('10) also speaks of the 'lingula' in the brains of the natives of India. The unusual prominence of this operculum coupled with the short fissura Sylvii may be interpreted as an index of the growth activity in the post-Sylvian region.

The anterior rami of the fissura Sylvii are in many instances difficult to identify; one brain in particular deserves mention. In both hemispheres the superficial appearance is of two

widely separated anterior rami, but in the right hemisphere the sulcus which corresponds in position with the ramus ascendens does not reach the limiting sulcus of the insula, consequently, according to Cunningham ('92), this sulcus is not an anterior ramus and cannot be homologous to the fissure of the opposite hemisphere occupying relatively the same position. This obvious inconsistency upholds the theory of Smith ('04) in regard to the formation of these rami. Another feature which lessens the value of data on these rami is the frequent thin opercular extension of the pars triangularis to the Sylvian fissure, giving rise to a merely superficial appearance of a separation or bifurcation of these rami.

There is positive evidence of an exposed insula in only one adult brain. The brain is that of a female and the condition is present in both hemispheres and is accompanied by an unusual simplicity of fissuration and a boldly curved fissura rhinalis. In several other hemispheres there is indication of defective development of the frontal operculum, but the insula is not sufficiently exposed to place them in the class with the one just mentioned.

The sulcus centralis presents no unusual features such as noted for the Sylvian fissure. The most prominent genu corresponds to the 'superior genu' of authors and is produced by a large rounded buttress of the gyrus centralis anterior. While a slight shallowing is noted at this level in a number of cases, there is no preference between the right and left hemispheres; comparing the male and the female shows a greater frequency of the condition in the male. The average height of this bridging gyrus above the floor of the fissure is 4.5 mm. Contrary to Cunningham's observation, the fetal brain of this series showed a very superficial bridging gyrus in both hemispheres.

Another point of disagreement with Cunningham's ('92) description of the sulcus centralis is in regard to the operculation of the gyrus postcentralis. He states:

> From the seventh month onwards the growth of the two bounding banks of the fissure does not proceed at an equal pace. There appears to be a greater growth energy in the posterior central convolution,

and this leads in the first instance to a greater prominence of the gyrus and ultimately to a partial overlapping of the frontal ascending convolution by the ascending parietal convolution. It is more obvious in the lower two-thirds of the fissure. It is owing to this that the adult fissure cuts into the cerebral surface in an oblique direction from before backwards.

From the study of this series of hemispheres the greater growth process appears to be in the gyrus centralis anterior and this gyrus is uniformly more prominent than the gyrus centralis posterior. There is a superficial appearance of an operculation by the gyrus centralis posterior, but this appearance is produced, not by overgrowth of the gyrus centralis posterior, but by the posterior extension of the gyrus centralis anterior in the deeper two-thirds of the fissure. This growth has displaced the floor of the sulcus centralis and so undermined the posterior gyrus. This quite clearly indicates that an apparent operculum does not always represent an excessive growth of the region. Further evidence of the greater growth energy of the anterior gyrus is seen in the prominence of the superior genu and the weakness of the inferior genu as shown in figure 3. This is in accord with Symington's ('13) observation "that the sinuous course of the fissure is secondary to growth in the anterior wall."

The data in regard to the superior and inferior termination of the sulcus centralis may be compared with those furnished by Cunningham and Retzius, although the value of such data is very doubtful. In 70 per cent of the hemispheres the sulcus cuts across the border and terminates on the mesial surface; Cunningham 60 per cent, Retzius 64 per cent. In 24 per cent the sulcus just reaches the border; Cunningham 21 per cent, Retzius 16 per cent. The fetal hemispheres possess a sulcus centralis which extends slightly beyond the border but at right angles to it, which suggests that the growth process which produces the typical diagonal arcuate sulcus centralis has not yet been completed.

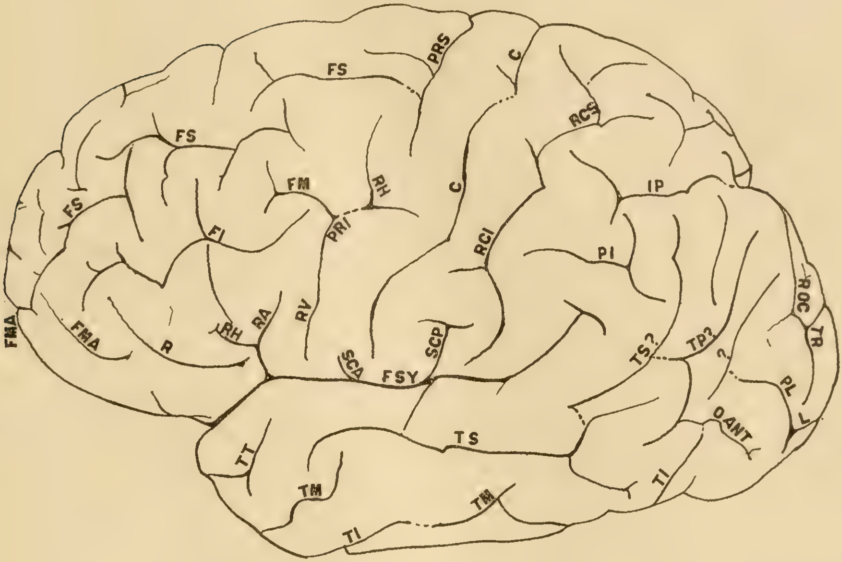
In only one hemisphere is there a very noticeable tendency toward the establishment of communications between the sulcus centralis and adjoining sulci. In this hemisphere there are

two connections with the sulcus praecentralis superior, one with the sulcus retrocentralis superior and one with the sulcus retrocentralis inferior. In the majority of the hemispheres the apparent communications are only shallow grooves. In six hemispheres there is a communication with the sulcus subcentralis anterior but in only two of these cases does the fissure extend to the Sylvian fissure, which is 8.3 per cent; Retzius found the condition in 16 per cent and Cunningham in 19 per cent.

The sulci praecentrales present no unusual features; the most common form is a complete separation of the two sulci by a superficial gyrus about 5 mm. in width. A union is present in 21 per cent. The sulcus praecentralis is united with the sulcus frontalis superior, as in figures 1 and 3, in 79 per cent of cases

ABBREVIATIONS

C, Sulcus centralis
CAL, Sulcus calcarinus
COL, Sulcus collateralis
D, Sulcus diagonalis
FI, Sulcus frontalis inferior
FM, Sulcus frontalis medius
FMA, Sulcus fronto-marginalis
FMED, Sulcus frontalis marginalis
FS, Sulcus frontalis superior
FSY, Fissura Sylvii
IP, Sulcus interparietalis
ISM, Sulcus interstriatus mesialis
L, Sulcus lunatus
LPR, Sulcus limitans precunei
LSS, Sulcus limitans area striata superior
OANT, Sulcus occipitalis anterior
OINF, Sulcus occipitalis inferior
PARC, Sulcus paracalcarinus
PI, Sulcus 'post-sylvius'
PL, Sulcus prelunatus
PO, Fossa parieto-occipitalis
POL, Sulcus occipitalis, pars polaris
PR, Sulcus precuneus
PRI, Sulcus praecentralis inferior
PRS, Sulcus praecentralis superior
R, Sulcus radiatus
RA, Fissura Sylvii, ramus asc. ant.
RCI, Sulcus retrocentralis inferior
RCS, Sulcus retrocentralis superior
RH, Fissura rhinalis
RO, Sulcus rostralis
ROC, Sulcus paraoccipitalis
RPD, Fissura Sylvii, ram. post. desc.
RT, Sulcus rostralis transversus.
RV, Sulcus praecentralis inferior, ram. transv.
SC, Sulcus cinguli
SCA, Sulcus subcentralis anterior
SCP, Sulcus subcentralis posterior
SP, Sulcus subparietalis
SRO, Sulcus subrostralis
TI, Sulcus temporalis inferior
TM, Sulcus temporalis medius
TP, Sulcus temporo-parietalis
TR, Sulcus transversus
TS, Sulcus temporalis superior
TT, Sulcus temporalis transversus
TTI, Sulcus temporalis transversus inferior



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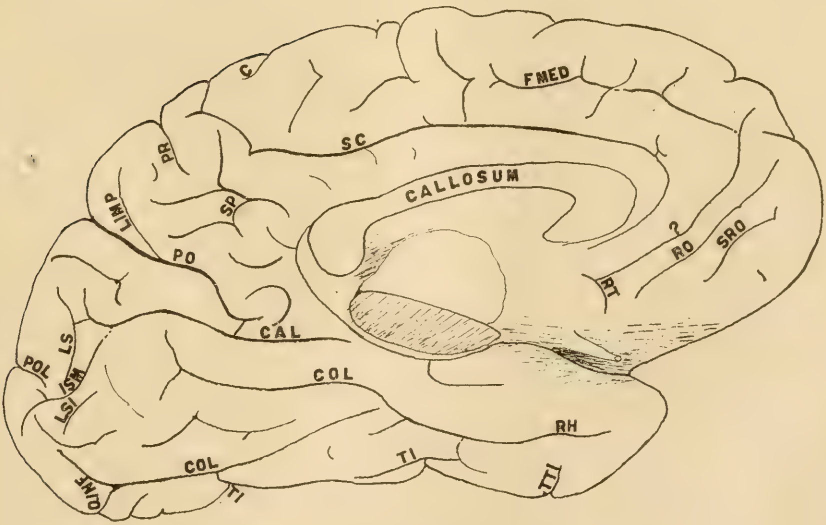

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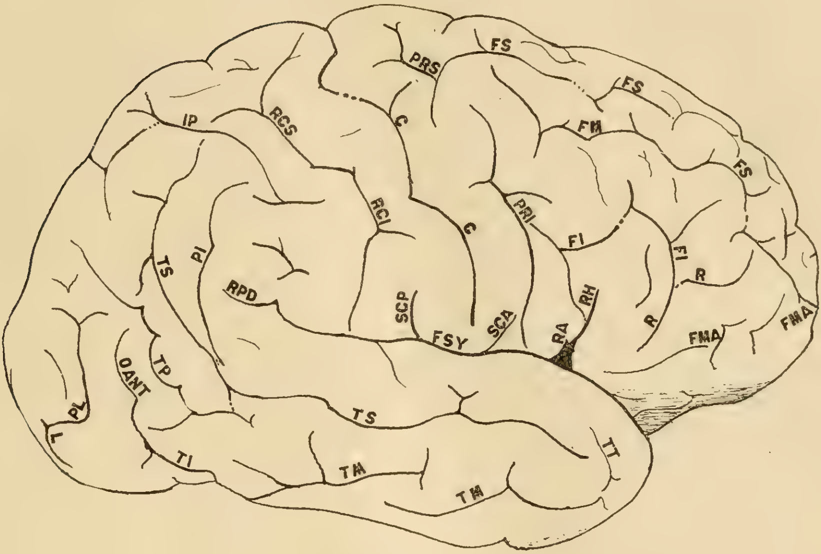
Fig. 1 Negro brain, male; left hemisphere; lateral view.
Fig. 2 Negro brain, male; left hemisphere; mesial view.

which compares favorably with other observations. The form of the sulcus praecentralis superior is very variable. A fairly constant posterior ramus has been described by Cunningham but was attributed by him to a posterior continuation of the sulcus frontalis superior. This sulcus which is represented in figures 3 and 5 may be more properly interpreted as a sulcus which has been called into existence by an excessive growth of the portion of the gyrus centralis anterior which gives rise to the superior genu of the sulcus centralis. In these cases it incises this prominent cortical region and gives to the gyrus an arcuate appearance.

The sulcus praecentralis marginalis and *sulcus praecentralis medius* are so inconstant and variable as to make observation on so small a number of hemispheres valueless.

The sulcus praecentralis inferior is much more strongly developed than the superior; in the majority of hemispheres it is represented by two elements, as shown in figure 3. It is connected with the fissura Sylvii in 41 per cent of cases as compared with 71 per cent given by Duckworth for Australian brains. A communication between the praecentralis inferior and the sulcus frontalis inferior occurs in 58.3 per cent.

The sulcus frontalis superior and the *sulcus frontalis medius* are discussed together because of their intimate association in the anterior part of the frontal lobe. The description of the sulcus frontalis superior as given by Cunningham and Retzius is not entirely in accord with the condition found in this series. The point of variation is the direction taken by the sulcus and the location of its anterior termination. If a line be drawn through the centers of the two or three elements, or if the sulcus is continuous following its general direction, this line will run parallel to the mesial border of the hemisphere at a distance from it of about 25 mm., and coincides with the juncture of the sulcus frontalis superior and the sulcus praecentralis superior posteriorly and anteriorly with the sulcus fronto-marginalis. While this difference in the position of the sulcus frontalis superior may be due in part to the interpretation of the anterior elements, yet the difference is so evident in the majority of hemispheres as



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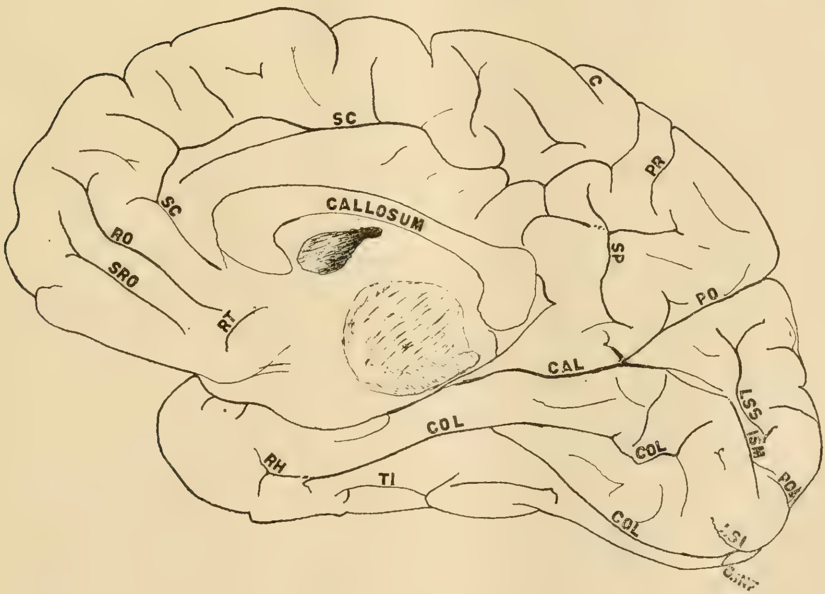

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Fig. 3 Negro brain, male; right hemisphere; lateral view.
Fig. 4 Negro brain, male; right hemisphere; mesial view.

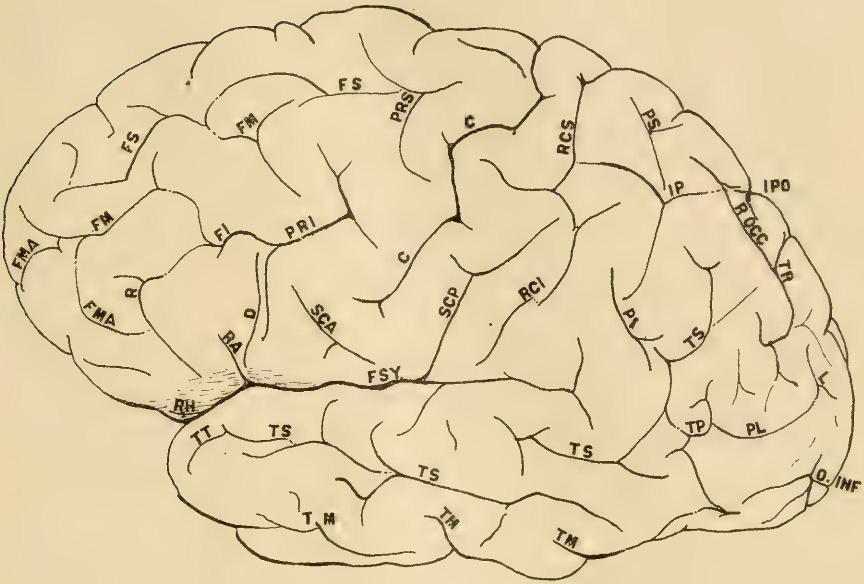
to force the conclusion that the gyrus frontalis superior in this series of brains is wider than in the average European brain and that the sulcus frontalis superior is more laterally placed. The continuous form of the sulcus frontalis superior in communication with the sulcus fronto-marginalis is found in 41 per cent. In the cases where the fissure is broken up there is some difficulty in interpreting the anterior element.

The sulcus frontalis medius is represented in the majority of hemispheres, 75 per cent, by several shallow irregular elements, and in very few is there a longitudinal sulcus indenting the gyrus. Figures 1, 3 and 5 illustrate the usual condition. There is nothing in the series to impress one with the importance attributed to the sulcus by Eberstaller ('90).

The sulcus frontalis inferior is characterized in this series of hemispheres by its great irregularity and its lack of conformity to any special type. The most frequent variety is that in which three elements are present, an anterior transverse, an intermediate horizontal and a posterior transverse. The last element in many instances cannot be distinguished from the praecentralis inferior, or sulcus diagonalis; communication with the latter occurs in 29.2 per cent of hemispheres.

The sulcus radiatus has been variously interpreted by authors; more recently the tendency has been to view the anterior bifurcation of the sulcus frontalis inferior as constituting the sulcus radiatus. The much greater frequency with which only two transverse elements occur in this region has probably been responsible for the interpretation. In this series this condition is present in 58 per cent of adult hemispheres. In the other hemispheres, as seen in figure 1, a detached inferior portion of the bifurcation might be considered a third transverse sulcus; from the evidence of the group we are lead to consider the posterior of the two transverse sulci usually found in this region as the sulcus radiatus, or anterior bifurcation of the sulcus frontalis inferior, and the anterior the lateral part of the sulcus fronto-marginalis.

The sulcus fronto-marginalis is represented by two quite distinct elements, a lateral and an internal. The lateral element



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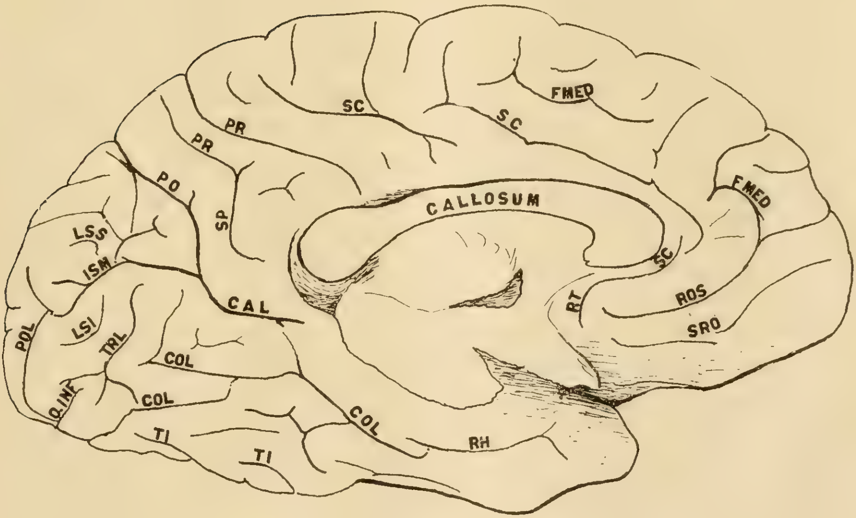

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Fig. 5 Negro brain, female; left hemisphere; lateral view.
Fig. 6 Negro brain, female; left hemisphere; mesial view.

has been noted in the description of the sulcus frontalis inferior. It is found in every hemisphere but one, which disagrees with Cunningham's statement that it occurs only in exceptional cases. In a few hemispheres it cuts across the supraciliary border to the orbital surface. In three cases it communicates with an internal element and so forms a superficially continuous sulcus extending from the frontal pole to the pars orbitalis of the gyrus frontalis inferior.

The internal element of the sulcus fronto-marginalis has been a topic for much discussion. The contention has been upon the identification of this sulcus with the sulcus rectus of lower apes, and from the evidence at hand the homology seems to be established. The explanation of the displacement of the sulcus rectus to a polar position occupied by the sulcus fronto-marginalis in the human brain involves a recognition of a growth process in the frontal lobe or frontal association area, which has resulted in a marked displacement of cortex and sulci towards the mesial border of the hemisphere. In this series the internal element of the sulcus fronto-marginalis can be divided in almost every instance into three parts, a posterior stem, an internal longer limb and an external shorter limb. Duckworth recognized this form in 71.4 per cent of Australian brains, however he found the external limb the longer in the majority of cases; he says ('07): "The fact that of these two terminal branches the outer is the longer more frequently than is the inner in Australian hemispheres, may be held to support Cunningham's view that the outer or lateral is developmentally the older, and the real continuation of the original sulcus."

This series of Negro hemispheres with the longer internal limb and its fuller and more direct continuity with the stem upholds the claim of the greater morphological importance of this part of the sulcus.

The sulcus diagonalis merits no special attention in this series; it is undoubtedly present in 50 per cent of hemispheres. In the remaining hemispheres it is represented in one of three ways, by an unusual inferior extension of the ramus verticalis of the sulcus praecentralis inferior, by a long inferior posterior limb

of the sulcus frontalis inferior or by a possibly misinterpreted ramus ascendens fissura Sylvii. A narrow sunken gyrus between the sulcus diagonalis and the sulcus praecentralis inferior is seen in several hemispheres and no doubt indicates a transition stage in the formation of the former sulcus.

The gyrus frontalis superior has already been noted on account of its great width; it may be added however that it is indented by a number of shallow elements which are identified as representing a sulcus frontalis mesialis. There is no definite or regular arrangement to these elements unless it is a greater tendency to a longitudinal direction in the posterior part of the gyrus and a transverse direction in the anterior region. In a small number of hemispheres a remarkable arrangement of longitudinal and transverse fissures suggests some governing factor in the production of these elements.

The mesial aspect of the gyrus frontalis superior is usually divided into two regions, a superior and a rostral, by a prominent anterior branch of the sulcus cinguli or by a transverse sulcus in the region, often in communication with the sulcus rostralis. The superior region is very variable in width and fissuration, dependent to a considerable extent upon the form and width of the lateral aspect of the gyrus frontalis superior. The sulci in this region are more frequently arranged in transverse series but may form an irregular longitudinal sulcus as seen in figure 2. The rostral region contains two fairly constant sulci, the sulcus rostralis and the sulcus subrostralis. In a small number of hemispheres an additional parallel sulcus is present; this is also seen in figure 2.

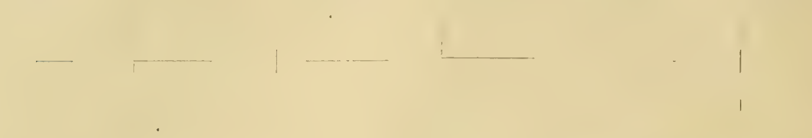
The orbital surface presents no distinguishing features; the most common form is a posterior transverse sulcus about 15 mm. in length which terminates at each extremity in a prominent posterior limb, and two or three anterior sagittal sulci which frequently communicate with it. A gyrus orbitalis transversus is so formed which is frequently incised by one or two branches from the Sylvian fossa.

The sulci retrocentralis and interparietalis will be considered together after the plan of Retzius, but it is very doubtful whether

there is any profit in analyzing the connections formed by these sulci. Table 1 presents the easiest way of comparing the conditions found in this series with the results of other observations.

TABLE 1

Type I *Type II* *Type III* *Type IV* *Type V* *Type VI*



Observation	Type per cents I	II	III	IV	V	VI
Cunningham	69	19	11	3	6.3	
Cunningham (Negro)	37	25	25		12	
Duckworth (Australian)		30	50			
Duckworth (embryo)	5.9	35.4	23.5		5.9	5.5
Retzius	55	11	17	4	9	4
Sernoff	44		31			
This series	66.6	21	25		4.2	

Complete union of all three elements without bridging gyri at any point in the complex was present in this series in only 8.5 per cent.

The inferences, if any, to be drawn from table 1 are in the main opposed to the conclusions of Cunningham in regard to the Negro brain, but in any case the difference between the Negro and the Caucasian is not enough to establish race characters.

The communication between the sulcus retrocentralis inferior and the fissura Sylvii is present in 21 per cent of hemispheres, it is generally effected through the sulcus subcentralis posterior.

The sulcus interparietalis is frequently deeper than the sulcus centralis, the average depth of the former is 21 mm. and of the latter is 20 mm. The bridging of the interparietal sulcus by a superficial gyrus occurs in 87.6 per cent, the condition amounts to an actual separation into two elements in 16.6 per cent. The ramus parietalis is quite variable in form but presents almost constantly a descending branch which incises the lobulus parietalis inferior and forms a boundary of the gyrus angularis and also frequently indicates its independence from the so called gyrus post-Sylvius. There is frequently a communication

between the ramus parietalis and the sulcus parietalis superior, obscuring the identity of the latter sulcus.

The ramus occipitalis shows in nearly every hemisphere the typical form of a sagittal arcuate sulcus with terminal anterior and posterior transverse bifurcations, the mesial limbs and body of which serve to define the gyrus arcuatus posterior; this can be well seen in figure 5. In no case is there a sharply defined bridging gyrus separating the sulcus transversus; in 16.6 per cent there is a possible communication with the sulcus lunatus. The mesial operculation caused by the lobulus parietalis inferior will be discussed later.

The sulcus lunatus, sulcus prelunatus and sulcus occipitalis will be discussed together on account of their intimate relationship. The findings in this region in this series of brains confirm in general the work of Smith. An examination of the extent of the area striata was not possible in every case; consequently the identification of the sulcus lunatus is in some instances less positive than it might otherwise be. There is a noticeably greater tendency to prominent and typical development in the left hemispheres; this accords with both Smith's ('04) and Murphy's ('10) observations. The area striata extends on to the lateral surface of the hemisphere in every case in which it was examined, but not to any great extent; its limit frequently coincides with one or two shallow grooves concentric with the sulcus lunatus.

The most interesting feature of this region is the unusual prominence of the sulcus prelunatus and the series of forms presented illustrating the mode of transition from a very short element to a typical sulcus occipitalis lateralis. It has an average length of 25 mm. and depth of 10 mm. It extends anteriorly to within a few millimeters of the ramus ascendens sulcus temporalis medius, and by its posterior communication with the sulcus lunatus, it forms an angle enclosing the lateral limb of the sulcus transversus. It thus forms a distinct boundary between the gyrus parietalis inferior and the gyrus occipitalis lateralis.

Smith seems to have considered the sulcus prelunatus and the sulcus occipitalis lateralis identical, but the conditions found in this series of Negro brains will not permit of such an interpretation. The more frequent method of forming the sulcus occipitalis lateralis is by a migration of one limb of the sulcus lunatus into line with the sulcus prelunatus proper, thus producing a long sulcus which extends to a point near the occipital pole parallel to the lateral border of the hemisphere. Two of the intermediate forms can be seen in figures 1 and 3; in the first figure the sulcus lunatus has migrated almost to the occipital pole but still retains a perpendicular communication at its center with the elongated sulcus prelunatus.

The sulcus occipitalis superior has been interpreted in this series as one or more sulci situated at or near the occipital pole between the sulcus lunatus and the bifurcation of the sulcus interstriatus mesialis, it might well be called the sulcus interstriatus lateralis. The typical Y-shaped form described by Smith is not found in these brains, but a fairly constant and very prominent sulcus is found at the occipital pole which perhaps represents a metamorphosed sulcus occipitalis superior. It is distinct in 46 per cent of hemispheres and has an average depth of 12 mm. There is frequently a shallow transverse communication with the sulcus interstriatus mesialis but this communication is evidently secondary and does not represent the gyrus cuneo-lingualis posterior. The anterior lip is quite distinctly operculated which, taken with the operculum of the posterior lip of the sulcus lunatus, would indicate a center of special growth activity in the lateral occipital region posterior to the lunate sulcus. Other evidence of the growth activity of this area is found in the operculum of the sulcus occipitalis inferior and the position of the sulcus occipitalis paramesialis on the mesial surface of the hemisphere.

The sulcus temporalis superior presents interesting features in both its anterior and posterior portions. A separate anterior element has been described as the sulcus temporalis transversus, which can be identified in 65 per cent of these hemispheres. In some cases it has a shallow communication with the main sulcus as seen in figures 1 and 3, in other cases the sulcus temporalis

superior seems to continue without interruption to the temporal pole in an arcuate course and with a markedly operculated inferior lip. The posterior extremity of the sulcus temporalis superior is in many instances situated far posterior in the lobulus parietalis inferior so that an unusually large and prominent area of cortex is found between the ramus ascendens and the sulcus retrocentralis inferior; this area will be referred to again in the summary. A fairly constant communication occurs between the sulcus temporalis superior and the ramus ascendens of the sulcus temporalis medius, sulcus temporo-parietalis of this study, it can be seen in figures 1, 3 and 5.

The sulcus temporalis medius is rarely found as a prominent single sulcus but is represented by three to five irregular diagonal elements. The anterior sulci are arranged in diagonal series extending from antero-superior to postero-inferior and frequently communicating across the border of the hemisphere with the sulcus temporalis inferior; the most anterior of these is frequently joined with the sulcus temporalis polaris. The posterior element is much larger and deeper than the preceding and runs in a different direction, for this reason it has been termed the sulcus temporo-parietalis. It has a fairly constant communication with the sulcus temporalis superior, and with the preoccipital element of the sulcus temporalis inferior, occasionally it is joined to the sulcus prelunatus or to the occipitalis inferior. In no case in this series was there found even a superficial communication with the diagonal elements of the sulcus temporalis medius.

The sulcus temporalis inferior is somewhat irregular in details but the series presents a general agreement in the number and position of the elements making up the fissural complex. Three elements are present; the anterior of these is a longitudinal sulcus situated a few millimeters lateral to the anterior extremity of the sulcus collateralis and frequently communicating with it. The posterior extremity of this element is joined to the second element in a small number of instances but a bridging gyrus is always present. The second element is situated opposite the central part of the sulcus collateralis near the lateral border of the hemisphere and frequently communicates with the other

elements of the sulcus. The third element is the deepest and most prominent of the three. In the great majority of cases it crosses the border of the hemisphere and communicates with the sulcus temporo-parietalis as already noted.

The sulcus cinguli has a very constant form in this series of hemispheres; Eberstaller's classification into three elements may be followed for the purpose of description but does not correspond to the conditions here presented. The greatest irregularity occurs in the anterior region, where it is often impossible to distinguish between a pars anterior and a sulcus rostralis or sulcus fronto-marginalis (fig. 6). The only point at which a definite division of the sulcus cinguli can be made out is at the junction of the anterior two-thirds and the posterior third. The pars posterior has a very inconstant form and is frequently represented, as in figure 6, by two or three diagonal elements.

The incisura cinguli appears to be the most constant feature of the complex. It has the superficial appearance of a continuation of the pars posterior sulcus cinguli across the mesial border of the hemisphere; an examination of the floor of the sulcus, however, reveals a condition somewhat comparable to that found in the fossa parieto-occipitalis. There appears to be a division in the depth of the sulcus which encloses a raised portion of cortex. The posterior branch of this division is the direct continuation of the sulcus proper and ends within the incisura. The lateral branch continues over the border and constitutes the 'paracentral sulcus.' The atypical cases of incisura are simply a wide separation of these two elements.

The lobulus precuneus does not present a regular form of fissuration. A more or less horizontal sulcus subparietalis is always present. The sulcus precuneus is represented by two or more elements, one of which cuts across the mesial border of the hemisphere in the majority of cases and forms an incising sulcus of the gyrus arcuatus medius of the lobulus parietalis superior. The marked operculation over the gyrus intercuneatus has already been noted.

The fossa parieto-occipitalis conforms in general to the description of Elliot Smith. The inferior portion of the fossa

seems to be more intimately related to the sulcus paracalcarinus than to the sulcus limitans precunei in 46 per cent of instances. The sulcus incisura parieto-occipitalis is the most variable and inconstant of the group. In some cases it is only represented by a pit, in others it lies almost entirely on the lateral surface as a mesial branch of the ramus occipitalis. Quite frequently a slightly sunken gyrus arcuatus posterior and operculated lobulus parietalis inferior produce a shallow communication of the sulcus incisura with the ramus occipitalis; this condition is very evident in both hemispheres of the fetal brain, probably because of the incomplete development of the gyrus arcuatus posterior.

The sulcus calcarinus presents great variations in form and depth. Spitzka has called special attention to the straightness of the combined sulcus in the Eskimos, a similar condition is noted in five of these hemispheres. In several others a marked superior convexity is seen, this is not due to the displacement of the floor of the sulcus but to the excessive growth of the inferior lip of the gyrus lingualis producing a prominent operculum which conceals a portion of the cuneus but which does not necessarily reduce its size. This operculum also conceals the communication with the fossa parieto-occipitalis and often gives rise to the superficial appearance of a direct continuity of the sulcus calcarinus and the fossa. In every instance an examination of the depth of this communication reveals a union of these two sulci at right angles to each other. The gyrus cuneus has been considered by some anthropologists an index of inferiority on account of its superficial appearance in some apes and its reported more superficial position in the Negro. In this series of Negro brains the gyrus cuneus can be made out in all but three hemispheres, but in the most prominent it lacks 10 mm. of reaching the superficial surface.

The sulcus interstriatus mesialis is variable. In 50 per cent of the hemispheres it terminates in the groove of the transverse sinus at the occipital pole. In no instance does it extend across the groove to the lateral surface. The lateral extension seems to be somewhat greater in the males than in the females. The bridging gyrus cuneolingualis posterior is present in 58 per cent,

and a posterior bifurcation can be recognized in 63 per cent of the cases. In several hemispheres a superficial appearance of bifurcation is a superior extension of the pars anterior of the sulcus to form the superior limb, while the pars posterior forms the inferior limb of the supposed bifurcation. Another source of error is the misinterpretation of the polar element of the sulcus occipitalis superior for the posterior bifurcation when there is a shallow communication between the two; such a condition is seen in figure 6.

It is noticeable that in all the hemispheres in which there is present a typical sulcus occipitalis lateralis, the sulcus interstriatus mesialis is very short. From a study of this series we are forced to conclude with Smith that "it is quite clear that the retrocalcarine sulcus of one brain is not necessarily strictly homologous with the retrocalcarine sulcus of another brain."

The sulcus collateralis is not a single sulcus but represents several elements which united or separate form a fissural complex. The only constant portion is the central element, and it is the only part which belongs strictly to the collateral sulcus. It is the deepest part of the complex and possesses a prominently operculated lateral lip. That this lip is of late development is shown by an examination of the fetal brain, in which it is absent, it is also absent from both hemispheres in the poorly developed female brain; there is a striking resemblance of the sulci collaterales of these two brains and very little resemblance to the forms present in the remainder of the series. In each the central element of the sulcus is shallow, non-operculated and terminates in an anterior arcuate bifurcation which is situated several millimeters posterior to a boldly curved fissura rhinalis.

The typical form of the sulcus as described by Retzius may be seen in figure 4; this condition is present in 40 per cent of the hemispheres. While the remaining hemispheres present a number of variations, they permit in general of the following interpretation. As has been said, the central element is constant. The anterior element in the great majority of cases represents a part of the fissura rhinalis, but it is incorrect to interpret it as entirely homologous to a portion of the fissura rhinalis. In

92 per cent of the hemispheres this rhinal element is indicated either by a complete separation or by a bridging gyrus at the point of union with the central element of the complex (sulcus collateralis). In the detached condition the element is seen to be made up of two parts joining at a wide but distinct angle. This angle corresponds in position to the shallow groove which marks the original course of the complete rhinal fissure. The continuation of this groove is the posterior limb of this rhinal element of the sulcus collateralis complex, and hence only this posterior limb is strictly homologous to a portion of the fissura rhinalis. The antero-lateral limb is an accessory branch brought into existence by the same growth process which produced the obliteration of the central portion of the fissura rhinalis. It would seem to be the most natural mechanical result of this growth process and its development is almost in direct proportion to the development of the bridging gyrus rhinencephalo-fusiformis. The proof of this statement is disclosed by an examination of the examples as they are arranged in figure 7; here we have a transition from a typical complete fissura rhinalis through the successive stages to the condition of an apparent continuous sulcus collateralis having no relation to the incisura temporalis.

The posterior part of the so-called sulcus collateralis is complex and difficult to interpret. Two separate modes of termination can be identified in this series of brains; the more common is a shallow communication by a long postero-lateral arm with a transverse sulcus in the region of the gyrus lingualis. There is, however, the greatest irregularity in the transverse sulcus and it evidently has a very secondary relation to the collateralis complex. The other mode of termination is by a superior arm which runs parallel to the sulcus calcarinus at a distance of about 10 mm., it crosses the mesial border of the hemisphere and frequently joins the calcarine-retrocalcarine angle, as seen in figures 2 and 6. In several hemispheres both of the above elements are present and then the termination is represented by a bifurcation; the frequency is 12.6 per cent.

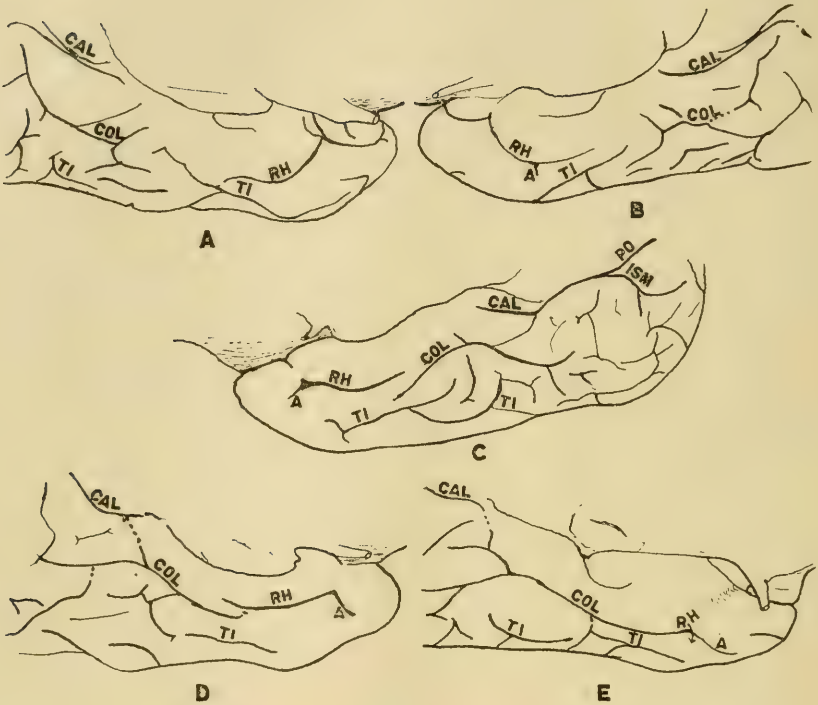


Fig. 7 A view of the tentoral surface, showing some variations of the sulcus collateralis and the fissura rhinalis. In A the sulcus collateralis and the fissura rhinalis are independent. B shows the fissura rhinalis still distinct but connected with an additional element, marked 'A'; this secondary element is brought into existence by some growth process which results in the obliteration of the central portion of the fissura rhinalis. C shows the anterior connection gone, the posterior end carried farther back and the antero-lateral element still present. D is another stage in advance and in E a union has occurred between the fissura rhinalis and the sulcus collateralis, the antero-lateral element is better developed and only a superficial groove marks the position of the internal portion of the fissura rhinalis.

SUMMARY

The frontal region has presented the greatest difficulty in the interpretation of the relation of the sulci to the cortical areas because the contrasts between adjoining areas are slight or impossible to detect. Such a relationship has been discovered in the occipital region and it is not unreasonable to suppose that similar, but as yet unidentified, factors have influenced the development and position of sulci in the frontal region. If we consider the center of the growth process to be in the frontal association area the result would be a migration of the surrounding sulci in all directions from this center with probable disintregation of some of them. Going still further, it can be conceived that the interaction between this growth center and that of the parietal association area has been partly responsible for the system of vertical sulci in the Rolandic region.

A growth activity in the frontal association area would affect the superior and inferior frontal regions. Downward expansion would result in a possible operculization to cover the insula, but might also force the sulcus frontalis inferior downwards until the gyrus frontalis inferior appeared less developed than before the growth occurred. The superior expansion would cause a migration of the sulcus frontalis superior towards the mesial border of the hemisphere, especially its anterior two-thirds. This would lead to a restriction of the lateral portion of the gyrus frontalis superior and to a decrease in the prominence of the sulcus frontalis mesialis. Similarly the sulcus fronto-marginalis would be effected, but the relation of this sulcus to the growth process is very similar to that of the sulcus occipitalis inferior in its region hence we may find disintegration as well as migration.

Viewed in the light of the above reasoning, this series of Negro brains presents a number of interesting features. As has been noted, the sulcus frontalis superior is almost invariably parallel to the mesial border of the hemisphere and frequently in communication with the sulcus fronto-marginalis; also in consequence of the unusually wide lateral aspect of the gyrus

frontalis superior, the sulcus frontalis mesialis is represented by a large number of elements and the sulcus frontalis medius is represented by a few shallow fissures.

The above condition is sufficiently striking to call for the attempted explanation of the causative factors, which have preceded the statement of these characteristics. If the explanation is correct, the findings would seem to substantiate the claims of a poorly developed frontal lobe or association area in the Negro brain, and would clear up a few confusing points in regard to the interpretation of the sulci in the frontal region. If the sulcus frontalis superior is situated relatively or actually further from the mesial border in the Negro brain than in the Caucasian and this is associated with a flattened anterior association center, this area must necessarily be smaller and not spread over a greater area in compensation for the flattening which might be due to the racial characters of the cranium.

Because the sulcus frontalis mesialis is absent in apes and present in man it was concluded by Cunningham ('92) and others that its simplicity indicated inferiority. In all probability it merely represents a human accessory sulcus whose complexity depends on the width of the gyrus frontalis superior. Since the width of this gyrus seems to vary inversely with the development of the anterior association center, the prominence of the sulcus frontalis mesialis would seem rather to be indicative of a poorly developed brain. In this series it is however too irregular to merit such distinction.

A general characteristic of the Negro brain which has been remarked by a number of observers, is the prominent parietal lobe in contrast to the 'ill filled' frontal region. In this series of brains it has been noted that the lobulus parietalis inferior presents a mushroom-like growth overlapping by operculi the surrounding cortex, especially in the region of the gyrus arcuatus posterior and gyrus arcuatus medius of the lobulus parietalis superior.

In the inferior parietal region there appears to be a variation from the generally accepted type of fissuration. A prominent accessory sulcus is found in the post-Sylvian region which in

over half of the hemispheres is too large to be passed over as a sulcus intermedius primus. This sulcus is undoubtedly a fissural representation of a prominent growth in the inferior parietal region. It has only a secondary morphological value, for it is absent in some of the hemispheres. It is noteworthy that in those hemispheres in which it is absent, the fissuration of the still prominent inferior parietal region is accomplished by one or two unusually prominent sulci intermedii in the posterior parietal region. From this it is safe to conclude that the presence of one or more very prominent accessory sulci in the inferior parietal region is a normal feature of the Negro brain, and that the greatest tendency, amounting to at least 75 per cent, is towards the development of this sulcus in the region between the posterior extremity of the Sylvian fissure and the ramus ascendens of the sulcus temporalis superior. When the sulcus is present its superior extremity is surrounded by a distinct and additional arcuate gyrus of the lobulus parietalis inferior, situated between the gyrus marginalis and the gyrus angularis. Probably this sulcus has been figured by Smith ('06, fig. 2).

Other minor variations have been noted in the preceding section but they are not of sufficient value to be reviewed.

We have refrained from the tabulation of characters supposed to represent Simian features, and which have been employed in some of the more recent studies. Many of these variations are due almost entirely to mechanical influences of a nature we can only suspect and are consequently unreliable as evidences of inferiority.

Some space has been devoted to the consideration of the occurrence of a detached portion of the fissura rhinalis, most frequently in communication with the sulcus collateralis. This reveals the fact that the apparent entire absence of the fissura rhinalis is in reality merely an interruption of this fissure by the superficial bridging gyrus fusiformis-rhinencephali. Therefore the degree of development of this fissure should be judged, not by the prominence of the incisura rhinalis, but by the prominence of the detached element of the fissura and the width or prominence of the bridging gyrus.

The sulci and gyri of the Negro brain are undoubtedly less complex and easier of interpretation than those of the Caucasian. But if, similar to brain weight, the complexity of fissuration is roughly indicative of intellect, it permits of only a very general comparison.

CONCLUSIONS

It is fully appreciated that conclusions drawn from the study of a small series of brains may be criticised on the ground of insufficient data, but the following will serve at least as an expression of the principal impressions gained from the review of the literature and the examination of this series of Negro brains.

There is an essential difference between the Negro and the Caucasian brain. This consists of a fairly constant variation of the Negro brain from an imaginary average type of fissuration obtained by a study of a large number of Caucasian brains. But the Negro type thus established lies within the limits of individual variation for the Caucasian, hence it is not possible to establish a single morphological feature which can be claimed as absolutely characteristic.

The relative characteristics of the Negro brain do not necessarily all denote inferiority or closer relation to the apes, but perhaps it is safe to say that the balance of evidence sustains the long held idea of the inferiority of the Negro.

This inferiority is expressed mainly in the frontal lobe by a flattened anterior association center representing actual deficiency of growth. This growth deficiency is farther evidenced by rostration, by the narrow gyrus frontalis medius and poorly developed sulcus frontalis medius, by the wide gyrus frontalis superior and by the irregularity of the fissures in the gyrus frontalis inferior. General features supposed to have a like significance are low average brain weight and generally greater simplicity of fissuration.

In the posterior association area activity of the growth process is expressed by a prominence of this region, by an operculation over the adjoining cortex and by the presence of a very prominent accessory sulcus in the region.

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THE MORPHOLOGY OF THE DIENCEPHALIC FLOOR

A CONTRIBUTION TO THE STUDY OF CRANIATE HOMOLOGY

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THIRTY FIGURES

The fact that the basal surface of the brain-stem is phyletically more constant in form than the lateral walls or the roof is so obvious as scarcely to need mention; yet in some respects it is a fact of considerable significance. It seems to have importance in estimating the homological values of certain parts of the basal region since this region in consequence of its greater morphological constancy should afford more exact evidence of homology. This becomes especially clear when it is considered how plastic are the lateral walls of the neural tube, not only in their embryonic development but in the adaptive modifications of which they are capable. A similar plasticity is seen in the roof-plate as witnessed by the varied conformation of the paraphysis, habenular region, epiphysis, mesencephalic tectum and cerebellum.

The basal region, on the other hand, is not without its variations; nor is it surprising that this region should bear traces of primitive characters, particularly in the interbrain, where the neural structures have always maintained such intimate relations to the stomadaeum, pituitary gland and branchial cavity. Andriezen (1), among others, has brought this fact out clearly. He observed in Ammocoetes, Amphioxus and Balanoglossus, as well as in the larval and adult forms of Ascidians, a small tubular aqueduct of capillary lumen and lined by ciliated epithelium, extending between the mouth cavity and the forebrain. This bucco-neural duct, he believes, provides a true water-vascular system for the central nervous

tissue. To the collection of ganglionic cells situated at the upper end of this duct he attributes a function similar to that of the osphradial organ in mollusca, thus bringing it into general relation with the olfactory apparatus. It is also his opinion that the hypophysis, in this sense, was functionally active in the ancestral vertebrates and that while the bucco-neural duct has been obliterated the sub-neural or pituitary gland with the collection of ganglionic cells has persisted. Ayers (2) is in accord with this theory when he states that the hypophysis arose as an organ of taste and the infundibulum was its nerve. Further evidence of this kind is furnished by Ganin (3), who was among the first to observe a connection between the anterior extremity of the embryonic neural tube and the branchial cavity in Ascidians. Similar observations were made upon chordata by Kowalevsky (4), Ussow (5), Julin (6) and von Kuppfer (7); the latter expressing himself as follows: "Der Verbindungskanal zwischen Hirn und Darm schlage ich vor als Canalis Neurentericus anterior zu bezeichen und die Glande hypophysaire von van Beneden und Julin wäre wohl am einfachsten als Neural-drüse zu benennen."

It seems probable in the light of these observations that such variations as do appear in the floor of the interbrain of craniates are adaptive in their nature. This idea is borne out by the fact that of all the structures arising from the diencephalic floor-plate the infundibular process is the most variable. This process from its early phases of development in all forms maintains close relation to the stomadaeum, pituitary evagination and branchial cavity. As an adult structure its modifications are numerous.

In the selachian (Mustelus laevis; fig. 1, A) the processus infundibuli projects caudad from the floor of the third ventricle; it presents two surfaces, i.e., a *ventral* or *pituitary surface* in contact with the pituitary gland, and a *dorsal* or *saccular surface* which is much convoluted and highly vascular forming the *saccus vasculosus*. In the amphibian (Rana pipiens; fig. 1, B) the same general relations obtain and the two characteristic surfaces are present except that the dorsal or saccular surface

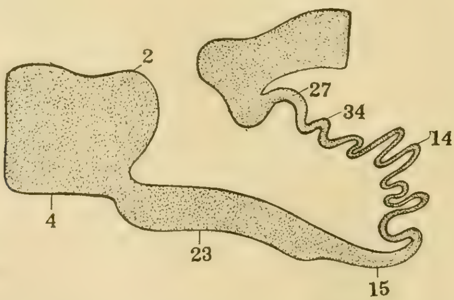
is less convoluted and less vascular, while the ventral one has increased in thickness.

In sauropsids, for birds as well as reptiles, the infundibular process differs in certain details from that of the ichthyopsid although the general homology of the structure in all these forms is discernible. In all three instances the cavity of the third ventricle extends into the infundibular process. In the selachian and amphibian this communication is not defined by any marked constriction. The bird (Gallus gallus; fig. 1, C) on the other hand, shows a distinct constriction in the region where the cavity of the general ventricular chamber passes over into the recess of the infundibular process. The process still presents its two characteristic surfaces: the pituitary surface is in contact with the pituitary gland, while the dorsal or saccular surface is much convoluted and non-vascular. This surface, unlike that in the frog and dog-fish, is thick. The recess of the infundibular process in the bird as in the other forms already described presents numerous branching diverticula.

The mammalian structure is characterized by a marked change in that the cavity of the third ventricle does not extend into the infundibular process which latter, in consequence, becomes solid except for a small proximal portion of its stem. These conditions are shown in the dog (fig. 1, E). So far as I am able to state at present one family alone, the Felidae, departs from the mammalian type in this respect. Here the third ventricle actually communicates with a large recess in the infundibular process by means of a narrow, tubular canal which passes from the ventricle through the stem of the process (fig. 1, D). The recess of the infundibular process shows no branching diverticula; the walls which bound it are thick and non-vascular, so that from all appearances it may be inferred that the convoluted saccular surface, so conspicuous in the selachian, amphibian and sauropsid, has been replaced by a now very extensive pituitary surface. This supposition is rendered more probable by the fact that the entire infundibular process in the mammal is completely invested by the tissue of the pituitary gland. In the anthropoids and man (fig. 1, F) the solidification

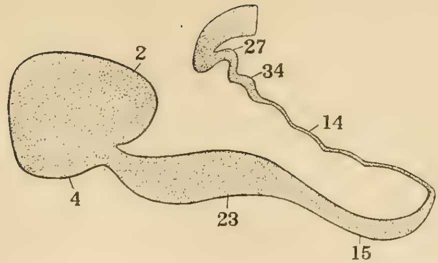
ANNOTATIONS FOR ALL FIGURES

1, Aqueduct of Sylvius
2, Chiasmatic process
3, Cerebellum
4, Chiasm
5, Corpus interpedunculare
6, Diverticula sacci vasculosi
7, Epiphysis
8, Ectoptic zone of Schulte
9, Foramen of Monro
10, Hypophyseal recess
11, Infundibular stem
12, Infundibular canal
13, Infundibular process
14, Infundibular process; saccular surface (saccus vasculosus)
15, Infundibular process; pituitary surface
16, Infundibular process, lateral process
17, Infundibular region
18, Infundibular evagination
19, Interoptic groove
20, Lamina terminalis
21, Lateral process of post-chiasmatic eminence (lobus inferior)
22, Lateral eminence
23, Median post-chiasmatic groove
24, Mid-brain
25, Mammillary region
26, Mammillary recess
27, Mammillary body (posterior lobe)
28, Neuropore
29, Optic vesicle or evagination
30, Optic peduncle
31, Optico-infundibular groove
32, Post-chiasmatic eminence (lobus inferior)
33, Post-chiasmatic recess (recess of inferior lobe)
34, Post-infundibular eminence
35, Post-infundibular recess
36, Post-infundibular evagination
37, Post-mammillary evagination
38, Prechiasmatic recess
39, Paraphysis
40, Recess of infundibular process or of infundibular evagination
41, Supraoptic crest
42, Supraoptic recess
43, Thalamencephalon
44, Telencephalon
45, Tuberculum postero-superius
46, Tubercle of the floor of Schulte
47, Velum transversum



1 A

Fig. 1 Comparative series of infundibular region. A, dog-fish; B, frog; C, fowl; D, cat; E, dog; F, man. *2*, chiasmatic process; *4*, chiasm; *14*, infundibular process, saccular surface; *15*, infundibular process, pituitary surface; *23*, median post-chiasmatic groove; *27*, mammillary body (posterior lobe); *34*, post-infundibular eminence.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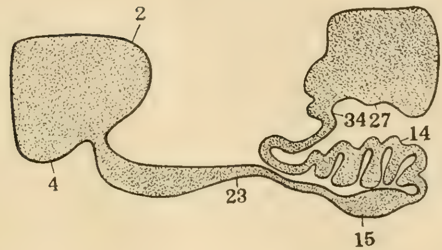
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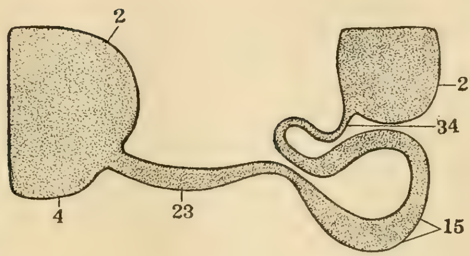
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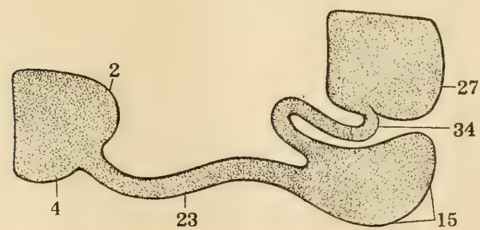
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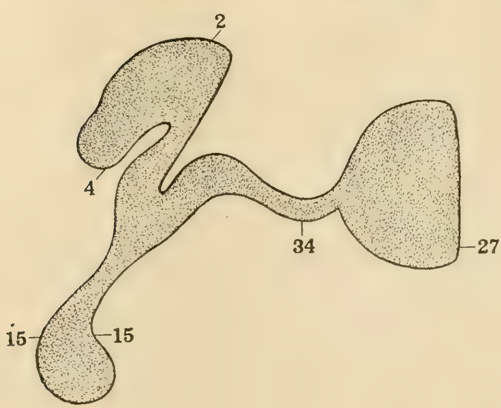
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1 F

of the infundibular process and the exclusion from it of any accessory recess of third ventricle have progressed to the most extreme degree, for in these forms even the stem of the process is solid.

In this way through a series of changes from the ichthyopsid to the mammal the evolution of the infundibular process may be traced. In this series the sauropsid condition still bears evidence of the saccus-formation in its apparently retrograding saccular surface; the conditions in the Felidae carry this retrograding process one step further toward the general mammalian type of infundibular process from which the saccular surface and the saccus-formation have entirely disappeared.

It is not, however, until the entire floor of the ventricle is considered that the significance of each of its several parts may be ultimately determined. These parts have been designated by many terms, several of which have been devised with the intention of giving a phylogenetic or embryological interpretation to the structures. Such, for example, is the case with the part described by Retzius (9) as the *eminentia saccularis*, for this term as applied to mammals imputes a genetic relationship between the eminence so described and the *saccus vasculosus* of fish. That such a relationship does not actually exist can, I think, be proved. For these reasons in considering this region of the brain it seems advisable to employ such terms only as shall be morphologically or topographically descriptive. To this end the following suggestions are offered for the structures found upon the floor of the third ventricle, beginning at the optic chiasm and proceeding caudad to the mammillary bodies:

1. The *optic chiasm*.

2. The *supraoptic crest*, a transverse ridge extending across the dorso-cephalic surface of the optic chiasm and for a short distance upon the optic nerves.

3. The *post-chiasmatic eminence*, a marked protuberance of the floor immediately caudad to the chiasm; this structure is often referred to as the *bulbus infundibuli*.

4. The *infundibular process*, an expanded appendage to the floor connected with the infundibular bulb by the *infundibular stem*.

5. The *post-infundibular eminence,* a small irregular and median protuberance in front of the corpora mammillaria and caudad to the infundibular bulb.

6. The *mammillary bodies.*

7. The *lateral eminences,* a pair of bilateral protuberances situated one cn either side of the post-chiasmatic eminence. Of these structures the post-chiasmatic, post-infundibular and lateral eminences constitute the *tuber cinereum,* while the infundibular process is appended to the tuber by the infundibular stem. In an earlier paper (8) the writer so interpreted the text and figures published by Retzius (9) as to assign the term eminentia saccularis to the post-chiasmatic eminence. Upon further investigation, however, it became obvious that Retzius referred to what is here called the post-infundibular eminence.

In the attempt to estimate the homological values of the structures in this region of the brain, serial sections obtained from the following adult forms were studied:

Squalus acanthias	Lepus sylvaticus	Canis latrans
Mustelus laevis	Sphingurus prehensilis	Canis familiaris
Lepidosteus osseus	Mephitis mephitica	Genetta vulgaris
Rana pipiens	Odocoelus hemionus	Felis domesticus
Menobranchus	Odocoelus virginianus	Felis pardus
Iguana tuberculata	Oryx beatrix	Felis leo
Gallus gallus	Ovis tragelaphus	Lemur macaco
Botaurus lentiginosus	Ovis aries	Macacus cynomolgus
Didelphys quica	Castor canadensis	Nyctipithecus trivirgatus
Bradypus tridactylus	Mirounga (Macrorhinus	Babuin cynocephalus
Dipus aegypticus	angustirostris)	Hylobates hoolock
Dasyprocta agouti	Nasua narica	Simia satyrus
Mus decumanus	Ursus horribilis	Homo

Studies of this portion of the neuraxis in the gross, even with the aid of the binocular, are quite unsatisfactory because of the compact arrangement of the structures which must be examined, and because dissection in this region can scarcely be performed without seriously disturbing the relation of the parts. For this reason, the Born method of reconstruction was employed in the study of the adult cat, dog, rat, rabbit, opossum, common fowl and dog-fish. It was also used in the reconstruction of models which demonstrate the ontogeny of the diencephalic structures in the cat, chick and dog-fish.

ELEMENTS IN THE DIENCEPHALIC FLOOR OF THE ADULT CAT

The lateral view of a model reconstructed to show the left side of the floor of the interbrain in an adult cat is reproduced in figure 2. At its cephalic extremity is the optic chiasm (*4*), while its most caudal structure is the mammillary body (*27*).

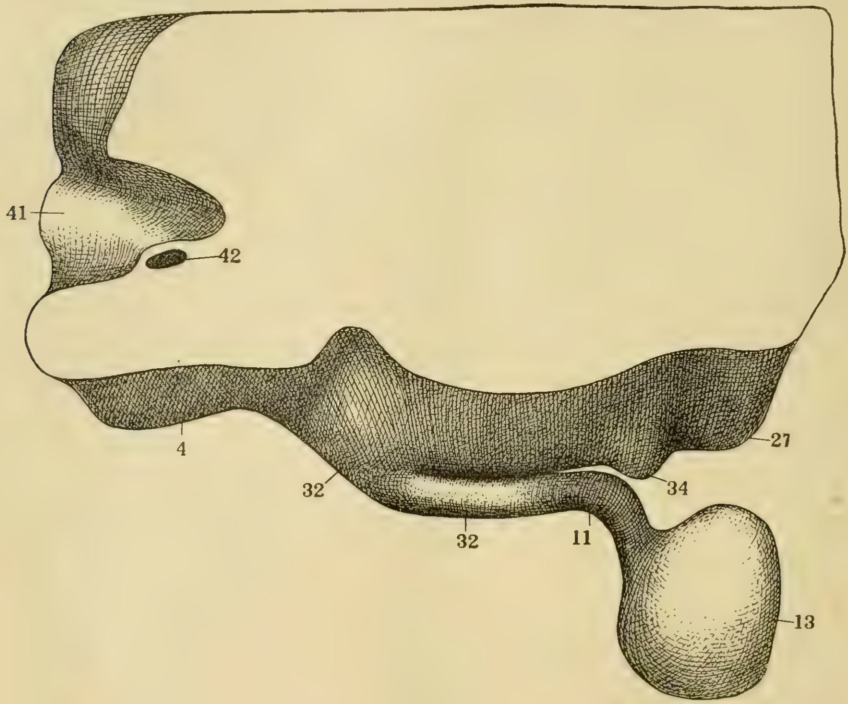

Fig. 2 Lateral view of forebrain reconstruction in adult cat. × 35. The unshaded area shows the cut surfaces of the reconstruction. *4*, chiasm; *11*, infundibular stem; *13*, infundibular process; *27*, mammillary body; *32*, post-chiasmatic eminence; *34*, post-infundibular eminence; *41*, supra-optic crest; *42*, supra-optic recess.

Above the optic chiasm and extending from the median line in either direction along the dorso-cephalic border of the chiasm and optic nerve is a ridge-like elevation, the supraoptic crest (*41*). This ridge is most prominent at and near the median line. It is most conspicuous in the carnivores, especially in the Felidae, but it is present in all the forms examined. The chiasm (*4*)

forms a well defined ridge crossing the outer surface of the floor, but immediately caudal to it is the largest protuberance of this region, the post-chiasmatic eminence or bulbus infundibuli (*32*). It is difficult to demonstrate this eminence on the actual brain, for the reason that it is almost entirely invested by a portion of the pituitary gland, the pars tuberalis. As a rule, this protuberance is torn away with the hypophysis when the attempt is made to study the structures in the floor of the third ventricle and such removal produces an artificial slit-like opening into the ventricle which has been called the *lura*. The post-chiasmatic eminence presents a long ventral surface which slants caudad and ventrad from the optic chiasm; it leaves the general plane of the floor at this level and proceeding for a considerable distance in the direction of the mammillary bodies reaches its greatest prominence about midway between these bodies and the chiasm. The ventral surface presents a shallow furrow whose long axis is in the median plane. This is the *median post-chiasmatic groove*. In this region the neural tissue forming the floor of the eminence is thin. Laterad in both directions the neural tissue rapidly increases in thickness; its ectal surface becoming convex forms two lateral processes of the post-chiasmatic eminence, one on either side of the median post-chiasmatic groove and each projecting free of the adjacent basal surface. The dorsal surface of the post-chiasmatic eminence is, in the main, parallel with its ventral surface but caudally it turns sharply upward to meet the plane of the floor. Two lateral borders bound the eminence, becoming more prominent as they are traced caudad; for about three-quarters of their distance they are divergent; they then become convergent caudad and as they approach each other form with the dorsal and ventral surfaces of the eminence a constricted stem-like prolongation, the infundibular stem (*11*) which projects caudad to become continuous with the expanded infundibular process (*13*). The infundibular stem and the infundibular process are invested by the pars infundibularis of the pituitary gland.

In all the other mammalian forms examined the post-chiasmatic eminence is a prominent feature of the diencephalon; it maintains

its definite relations to the pars tuberalis, and appears with but slight variations in the same general conformation as described in the cat. The most considerable modifications in its form are seen in the anthropoids and man. In these forms it does not hold the same relation to the floor of the interbrain as in the lower mammals. This change is occasioned by the forward and downward rotation which occurs in the hypophysis as the latter sinks into the deepened sella turcica. Another factor operative in this change is the foreshortening of the sella in man and the apes which further tends to force the pituitary gland craniad. The rotation from the developmental standpoint seems to be secondary to the increased depth in the pituitary fossa, for in the five-month human fetus, as the writer has previously shown (8), the post-chiasmatic eminence occupies a position corresponding in all details to that of the adult cat. It is only in the late fetal and early post-natal stages that the protuberance undergoes a change in relations which in effect is the result of a rotation of the hypophysis through 90°. When this is completed the surface described in the cat and other mammals as ventral no longer presents a ventral inclination but is turned craniad, while the eminence as a whole has become elongated in its long axis and constricted transversely. As a result it has a more or less bulbous appearance, a fact which has given rise to the term *bulbus infundibuli*.

The most caudal structures entering into the floor of the third ventricle are the corpora mammillaria (*27*); the one on the left side is shown in figure 2. In the adult cat these bodies are large protuberances situated one on either side of the median line and immediately cephalad to the posterior perforated space. They appear in all the mammals studied and are also present though less conspicuous in sauropsid forms.

The post-infundibular eminence (*34*) occupies a position immediately in front of the mammillary bodies. In lateral view (fig. 2) it does not appear so prominent as the latter structures nor has it the sharp lateral demarcation of the corpora. On the other hand, it is definite in all mammals. So far as may be stated upon the evidence of the material examined it is most

conspicuous in carnivores. In primates it is not always well marked, yet in all the apes examined it was present. In man, especially in later adult life, considerable care may be required to detect it, although in many instances it is quite as evident as in the carnivores; this is particularly true in the brain of the infant and child. The eminence appears in ungulates; at least it was observed in several varieties of artiodactyla (sheep, mountain goat, mule deer, aoudad and Virginia deer). It is prominent in the proboscidea (Indian elephant) and also occurs in rodents and marsupials. The post-infundibular eminence appears as a transverse ridge extending across the ventricular floor. It is most prominent at and near the median line; it presents no sagittal division into bilateral halves and laterally merges with the general plane of the basal region. Its shape is somewhat variable; often it is elongated cephalo-caudad and it may be asymmetrical. Its ventral surface may arise sharply to the floor of the ventricle or it may blend gradually with this area. Its caudal surface usually rises abruptly to the ventricular floor.

The developmental history of the post-chiasmatic eminence shows that it is partially constricted off from the basal portion of the interbrain by the growth of the pars tuberalis of the pituitary gland. Two basal regions thus lie above the eminence, symmetrically placed, one on either side of the median line. In shape they are roughly triangular having their bases turned mesad and their apices projecting laterally. The base of each triangle extends from the post-infundibular eminence almost as far forward as the chiasm. As they are followed laterad each presents a protuberance which is most pronounced near the apex of the triangle. These protuberances and the basal areas with which they are in continuation constitute the lateral eminences (*22*).

The median sagittal view of the model reconstructed from the diencephalic floor in the adult cat is shown in figure 3. This view gives the ventricular recesses many of whose surface expressions have already been discussed. Cephalad to the chiasm (*4*) the ventricular cavity extends forward and slightly down-

ward as the small prechiasmatic recess (*38*) which corresponds to the median portion of the supraoptic crest (*41*). This recess is continued laterad as a long canal extending for some distance above the optic nerve, the supraoptic recess (*42*). Both the prechiasmatic and supraoptic recesses are present in all the forms

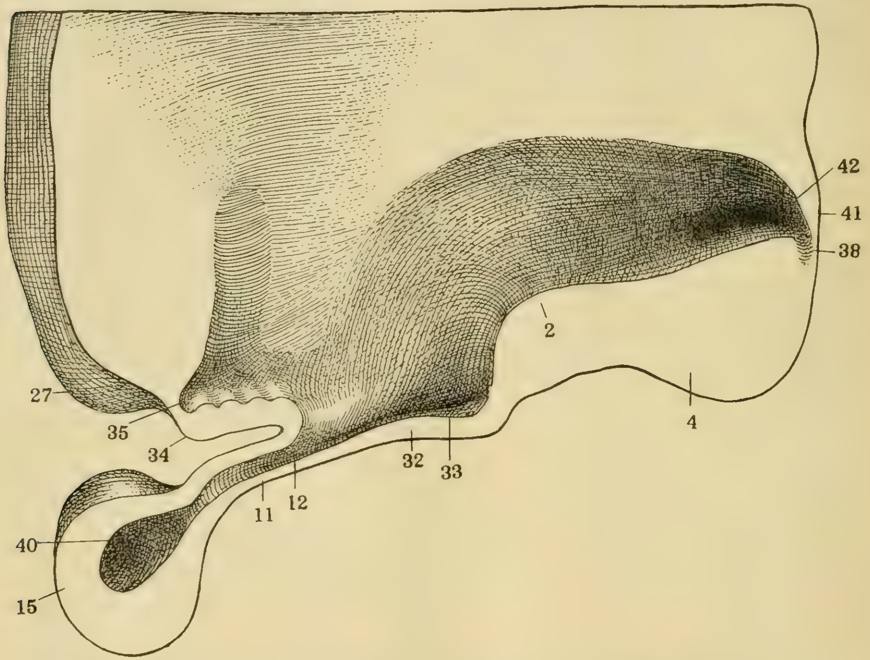

Fig. 3 Mesial view of forebrain reconstruction in adult cat. × 35. The unshaded area shows the cut surfaces of the reconstruction. *2*, chiasmatic process; *4*, chiasm; *11*, infundibular stem; *12*, infundibular canal; *15*, infundibular process, pituitary surface; *27*, mammillary body; *32*, post-chiasmatic eminence; *33*, post-chiasmatic recess; *34*, post-infundibular eminence; *35*, post-infundibular recess; *38*, pre-chiasmatic recess; *40*, recess of the infundibular process; *41*, supra-optic crest; *42*, supra-optic recess.

examined. Caudal to the prechiasmatic recess a large prominence rises from the floor of the ventricle in a position corresponding to the optic chiasm. This is the chiasmatic process (*2*). From the caudal extremity of this process the floor falls sharply away and then extends backward for a considerable distance with a marked ventral inclination. The slope thus

formed has its surface expression in the post-chiasmatic eminence and consequently this portion of the ventricular cavity is the post-chiasmatic recess (*33*). This recess extends laterally on either side of the median line forming an expanded portion of the ventricular cavity. As it is followed caudad the post-chiasmatic recess becomes constricted until it forms a tubular canal, the infundibular canal (*12*), which passes through the infundibular stem to communicate with the cavity of the infundibular process, the recessus processi infundibuli (*40*). The post-chiasmatic recess and the infundibular canal were present in all the forms examined but the distance to which the canal penetrates the infundibular stem is variable. In the Felidae it passes through the entire length of the stem while in all other carnivores it extends a short distance only. It is shortest in ungulates, anthropoids and man, although in these forms the infundibular stem attains its greatest length. The recess of the infundibular process is present, so far as I am at present able to state concerning mammals, in the Felidae alone. In these forms it is in direct communication with the third ventricle through the infundibular canal. In such birds and reptiles as I have studied it is present as a cavity having numerous accessory diverticula. The general conformation of this recess and the infundibular process which contains it have already been discussed (page 214).

As the dorsal surface of the post-chiasmatic eminence (*32*) ascends and reaches the plane of the floor, it becomes continuous with an area whose external expression is the ventral surface of the post-infundibular eminence (*34*). Entally this area presents several transverse ridges which separate two or three rather well marked grooves extending transversely across the floor of this region. Caudal to these folds the floor-plate becomes smooth and laterally a conspicuous sinus or recess situated in front of the mammillary recess appears in all the mammals studied. Like several of the other structures already mentioned, it is a most conspicuous element in the Felidae.

THE DIENCEPHALIC FLOOR OF THE ADULT FOWL (GALLUS GALLUS)

All of the eminences appearing in the cat may be identified in the fowl (fig. 4). The supraoptic crest (*41*) is present as a ridge extending laterad along the dorso-cephalic border of the chiasm toward the optic nerve. It marks the position of the supraoptic recess (*42*) of the third ventricle. Caudad to the chiasm the diencephalic floor forms a prominent post-chiasmatic eminence (*32*) which, as in the case of mammals, is invested by the tuberal portion of the pituitary gland and contains the post-chiasmatic recess (*33*). From the caudal extremity of this eminence projects the infundibular stem (*11*) terminating in the infundibular process (*13*). In the bird and the reptile this process presents certain features which distinguish it from that of the mammal. It is broader and each lateral extremity is prolonged to form a slender lateral process (*16*) similar to the lateral process of the selachian. Equally characteristic are the two surfaces of the infundibular process, i.e., the pituitary (*15*) and saccular (*14*) surfaces; the former is in contact with the pituitary gland; the latter has no such relation but presents many irregular convolutions. Its wall is thick and non-vascular. As the saccular surface of the infundibular process ascends and approaches the general plane of the ventricular floor it becomes evaginated to form a diverticulum, the post-infundibular eminence (*34*). This structure seems to present features in which it differs from the post-infundibular eminence in the cat. It appears to be a constituent of the post-chiasmatic eminence rather than being directly in the floor of the ventricle as in mammals. In Botaurus lentiginosus (shown in fig. 5) it more closely resembles the mammalian conditions. The avian third ventricle is in general much more narrow than in other forms. Only in its cephalic extremity does it broaden out to establish free communication with the large prechiasmatic and post-chiasmatic recesses. In the interthalamic portion of the ventricle in the fowl the walls are in close apposition; the extent of the cavity in this region is further limited by the unusual size of the tuberculum postero-superius which projects cephalad for a

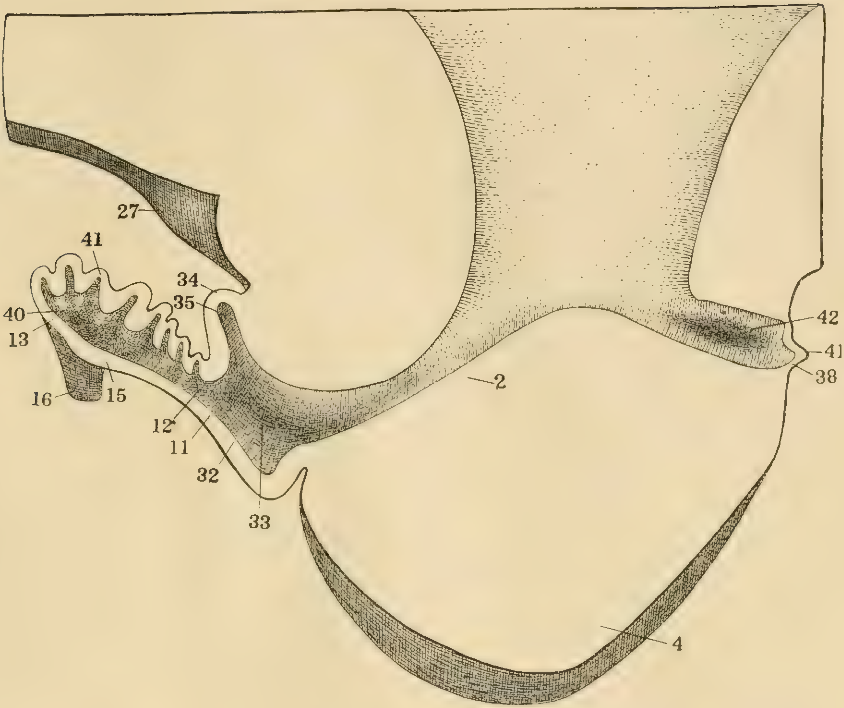

Fig. 4 Mesial view of forebrain reconstruction in adult fowl (Gallus gallus). × 50. The unshaded area shows the cut surfaces of the reconstruction. *2*, chiasmatic process; *4*, chiasm; *11*, infundibular stem; *12*, infundibular canal; *13*, infundibular process; *14*, infundibular process, saccular surface; *15*, infundibular process, pituitary surface; *16*, infundibular process (lateral process); *27*, mammillary body; *32*, post-chiasmatic eminence; *33*, post-chiasmatic recess; *34*, post-infundibular eminence; *35*, post-infundibular recess; *38*, pre-chiasmatic recess; *40*, recess of the infundibular process; *41*, supra-optic crest; *42*, supra-optic recess.

considerable distance into the ventricular chamber. The hypothalamic portion of the ventricle extends caudad beneath the ventral surface of the massive tuberculum postero-superius; for this reason the caudal portion of the post-chiasmatic eminence and the post-infundibular eminence appear to be appendages to rather than constituents in the floor of the third ventricle of the fowl. In the bittern (fig. 5), on the other hand, the post-infundibular eminence is in the ventricular floor while the

infundibular process projects caudad as an appendage of the postchiasmatic eminence. Both the optic chiasm (*4*) and the chiasmatic process (*2*) in the fowl are prominent and the pre-chiasmatic recess (*38*) is correspondingly deep. In its general features the post-chiasmatic eminence (*32*) is similar to that in the cat. It has a long transverse axis. Its ventral surface presents a longitudinal furrow, the long axis of which is in the median line.

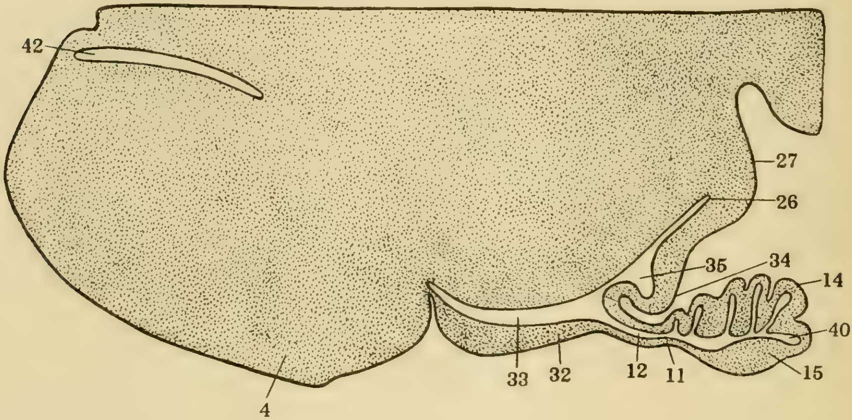

Fig. 5 Sagittal section of Botaurus lentiginosus in region of interbrain. *4*, chiasm; *11*, infundibular stem; *12*, infundibular canal; *14*, infundibular process, saccular surface; *15*, infundibular process, pituitary surface; *26*, mammillary recess; *27*, mammillary body; *34*, post-infundibular eminence; *35*, post-infundibular recess; *40*, recess of infundibular process; *42*, supra-optic recess.

This is the median post-chiasmatic groove. Here the neural tissue is relatively thin. Extending laterad in both directions from this groove the surface of the eminence becomes convex while the neural tissue rapidly increases in thickness until it forms the prominent lateral processes (*21*) of the post-chiasmatic eminence which project free of the diencephalic floor. The general plane of the post-chiasmatic recess (*33*) is at right angles to the interthalamic portion of the ventricle and follows the ectal contour of the post-chiasmatic eminence. The infundibular canal (*12*) is short and narrow; it communicates directly with the recess of the infundibular process (*40*). The latter presents dorsally a number of minute tubular canals which

project into the corresponding diverticula sacci vasculosi (*6*). These tubular canals open ventrally into a larger subdivision of the recessus processi infundibuli which is in relation to the pituitary surface of the infundibular process, the hypophyseal recess (*10*). Laterally the hypophyseal recess may be traced into the two tapering lateral processes (*16*) of the infundibular process. The post-infundibular recess (*35*) communicates with the post-chiasmatic recess in a position slightly dorsal to the infundibular canal. In the fowl the mammillary bodies (*27*) are partly concealed by the post-infundibular eminence but appear as slight elevations in the floor dorso-lateral to this structure. Because of this relation they seem to be situated at some little distance from the median line on either side having the post-infundibular eminence and its recess interposed between them. They contain no mammillary recess in the fowl. In the bittern the mammillary bodies are dorso-caudad to the post-infundibular eminence and occupy a position much nearer to the median line than in the fowl. A small mammillary recess extends for a short distance into the mammillary body in this form (fig. 5).

THE DIENCEPHALIC FLOOR OF THE ADULT SELACHIAN (MUSTELUS LAEVIS)

The mesial view of a model reconstructed to show the left half of the interbrain floor in the adult Mustelus laevis is reproduced in figure 6. Of the elements entering into the floor the lamina terminalis (*20*) is the most cephalic. The optic chiasm (*4*) is caudal to the supraoptic crest (*41*) which extends transversely across the dorso-cephalic surface of the chiasm, and may be followed for a short distance out upon the optic nerve. Caudal to the chiasm is the post-chiasmatic eminence which differs in certain particulars from the corresponding region of the mammal and sauropsid, although it occupies the same topographical position. The chief points of difference arise from the facts that the three divisions of the post-chiasmatic eminence in the dog-fish are more pronounced than in the

cat and fowl and at the same time this region is a relatively much more expansive area than in the forms already mentioned. Two of its divisions are bilaterally symmetrical in the form of large ovoid protuberances situated one on either side of a smaller median area. The lateral protuberances are the *lobi inferiores* (*21*); they correspond in position to the lateral processes of the

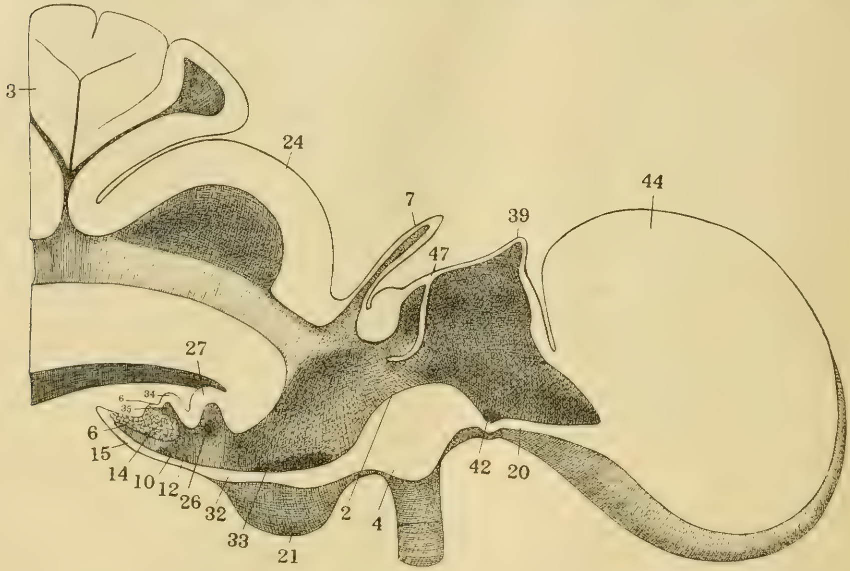

Fig. 6 Mesial view of brain reconstruction in adult Mustelus laevis. × 25. The unshaded area shows the cut surfaces of the reconstruction. *2*, chiasmatic process; *3*, cerebellum; *4*, chiasm; *6*, diverticular sacci vasculosi; *7*, epiphysis; *10*, hypophysial recess; *12*, infundibular canal; *14*, infundibular process, saccular surface; *15*, infundibular process, pituitary surface; *20*, lamina terminalis; *21*, median chiasmatic groove; *24*, mid-brain; *26*, mammillary recess (recess of posterior lobe); *27*, mammillary body (posterior lobe); *32*, post-chiasmatic eminence (inferior lobe); *33*, post-chiasmatic recess (recess of inferior lobe); *34*, post-infundibular eminence; *35*, post-infundibular recess; *39*, paraphysis; *42*, supra-optic recess; *44*, telencephalon; *47*, velum transversum.

post-chiasmatic eminence in birds and mammals; they are not invested by or in contact with the pituitary gland. The small median area corresponds to the median post-chiasmatic groove (*23*); it is contiguous with a relatively long, tongue-like process of the pituitary gland, the developmental history of which latter

gives it all the characteristics of the mammalian and sauropsidan pars tuberalis. In the bird and mammal the caudal extremity of the post-chiasmatic eminence becomes constricted to form the infundibular stem (*11*), but in the selachian this constriction is less marked so that the stem is wide and short. It is difficult to appreciate it at all except by means of reconstruction. At its caudal extremity the stem becomes rapidly expanded to form the spacious infundibular process (*13*). This process presents two characteristic surfaces, i.e., a ventral one which is smooth and in contact with the pituitary gland, the pituitary surface; and a dorsal convoluted saccular surface, membranous in character and highly vascular. This latter forms the *saccus vasculosus*.

Dorsal to the saccus vasculosus is a small protuberance which differs structurally from the saccus in that it is composed chiefly of neural tissue. This is the post-infundibular eminence (*34*), dorsal to which is a larger protuberance, the *posterior lobe* (*27*). This structure forms a prominent eminence at the point of juncture between the mid-brain and the interbrain. Laterally its extremities project free of the adjacent neural tissue. These lateral extremities are in connection with a less protuberant median portion of the lobe. The transverse diameter of the lobus posterior is about twice that of the infundibular eminence; both protuberances are symmetrically disposed with reference to the mid-sagittal plane. Cephalad the recess of the posterior lobe is in direct communication with the diencephalic ventricle; caudad it opens into the post-infundibular recess (*35*). The recess of the infundibular process (*40*) is bounded ventrally by the pituitary surface of the infundibular process, while caudo-dorsally it is limited by the saccular surface forming the saccus vasculosus. This surface is thrown into a number of convoluted folds thus producing the diverticula sacci vasculosi (*6*). Ventral to the saccus vasculosus the infundibular recess presents a marked subdivision, the hypophyseal recess (*10*), while both the pituitary and saccular surfaces are so prolonged laterad as to form two long tapering processes, each of which contains a lateral extension of the infundibular recess. Corre-

sponding to the short, broad infundibular stem, the infundibular canal (*12*) is not well defined, although it may be recognized as a slight constriction occurring dorsad at the area of transition between the saccus vasculosus and the post-infundibular eminence and ventrad in the region in which the pituitary surface of the infundibular process passes into the median post-chiasmatic groove (*23*). The post-chiasmatic recess (*33*) corresponds in its subdivisions to the post-chiasmatic eminence, there being two large lateral diverticula extending into the inferior lobes in connection with a median canal which communicates cephalad with the suprachiasmatic portion of the third ventricle and caudad with the recess of the infundibular process. Cephalad to the post-chiasmatic eminence the ventricular floor is elevated above the chiasm to form the chiasmatic process (*2*) which passes across the floor as a prominent transverse ridge. The dorso-cephalic surface of this ridge becomes rapidly depressed as it proceeds cephalad, and in the mid-sagittal plane becomes the caudal boundary of the prechiasmatic recess (*38*).

Traced laterad this recess leads into a small tubular canal which extends for some distance above the optic nerve, the supraoptic recess (*42*). In the selachian the lamina terminalis (*20*) occupies a nearly horizontal plane, extending with a slight dorsocephalic inclination from the prechiasmatic recess to the corpus striatum.

EMBRYOLOGICAL ANALYSIS OF THE DIENCEPHALIC FLOOR IN THE CAT, CHICK AND DOG-FISH

The following analysis of the floor of the interbrain is based upon some recent work of Prof. H. von W. Schulte (12), in which the writer collaborated.[1] It is shown in this study that the fore-brain in the cat consists of two primitive elements, the optic vesicles and the mammillary region. The latter persists with but little alteration until a relatively late period. The primi-

[1] In connection with this work it gives me pleasure to express my indebtedness to Professor Schulte for, although it was my privilege to collaborate with him in the study of the early development of the brain in the domestic cat, the new ontogenetic interpretation resulting from this investigation originated with him.

tive optic vesicles early become profoundly remodelled giving rise to a much reduced optic evagination and a pronounced area of the neural wall which surrounds it. This area is called the *ectoptic zone.* It presents itself as an arc of three distinct segments, the dorsal segment giving rise to the thalamencephalon, the cephalic segment to the telencephalon and the ventral segment to the infundibular region. All of these secondary derivatives are present in the cat embryo of twenty-one somites (see fig. xxxviii in loc. cit.).

Development of the diencephalic floor of the cat

Cat embryo of 4.5 mm.; twenty-six somites; Specimen No. 495 (fig. 7). The forebrain of this embryo shows an advance over the conditions observed in the embryo of twenty-one somites. All of the primitive elements of the prosencephalon previously described may be recognized. The optic vesicles (*29*) are further reduced in size, and present a constriction at their point of attachment to the neural tube. Their external configuration is still convex upon all surfaces. The ectoptic zone shows its characteristic division into thalamencephalon (*43*), telencephalon (*44*) and infundibular region (*17*). The regio mammillaris (*25*) is well marked and ectally separated from the apex of the infundibular region by a shallow transverse furrow, the tubercle of the floor (*46*).

The most pronounced changes are evident in the regio infundibularis, not only in the fact that this region is enlarged but also because it presents two subdivisions, both evolved from the apex of this area. The first of these subdivisions appears as a ventral protrusion which is conical in shape, the infundibular evagination (*18*). Dorsal and caudal to this appears a large, shallow diverticulum which, because of its position, may be designated the post-infundibular evagination (*36*). The remainder of the infundibular region forms the greater part of the floor of the prosencephalic ventricle. Its general plane of inclination is caudo-ventral, and its thickness is uniform throughout its entire extent. Entally it presents on either side a deep groove passing along the lateral wall from the now circular orifice of the optic

vesicle to the apex of the infundibular region. This is the optico-infundibular groove (*31*). It occupies relatively the same position as the horizontal limb of the primitive optic sulcus. Its increased prominence upon the ental surface of the ventricular wall appears to have occasioned a corresponding ridge upon the ectal surface, the optico-infundibular ridge.

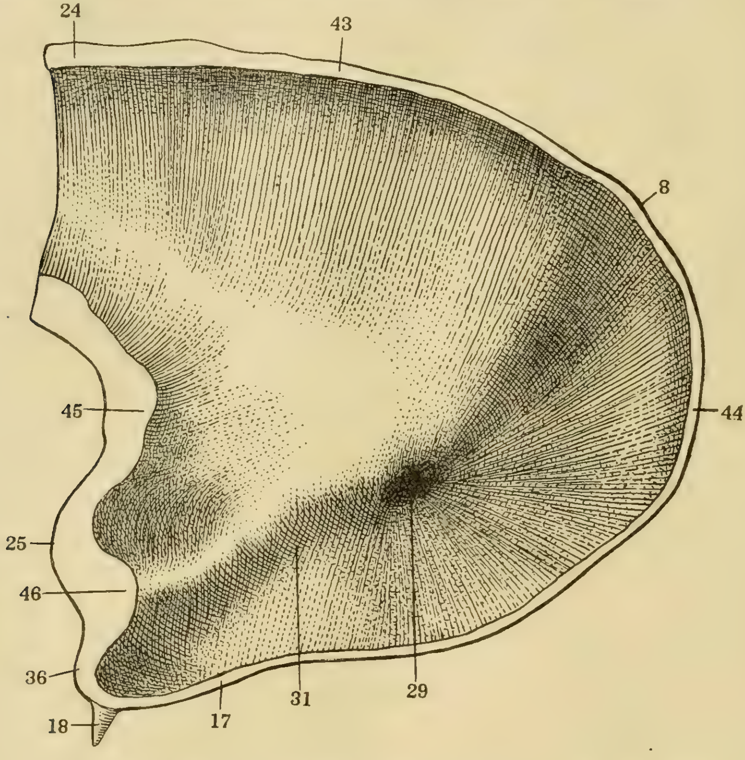

Fig. 7 Mesial view of forebrain reconstruction of a 4.5 mm. cat embryo (26 somites). × 150. The unshaded area shows the cut surfaces of the reconstruction. *8*, ectoptic zone of Schulte; *17*, infundibular region; *18*, infundibular evagination; *24*, mid-brain; *25*, mammillary evagination; *29*, optic evagination; *31*, optico-infundibular groove; *36*, post-infundibular eminence; *43*, thalamencephalon; *44*, telencephalon; *46*, tubercle of the floor of Schulte.

The mammillary region, although increased in size as compared with the earlier stages, manifests no other changes. Dorsal to it is the tuberculum postero-superius (*45*), while ventrad is

the floor tubercle of Schulte (*46*), the tuberculum postero-inferius.

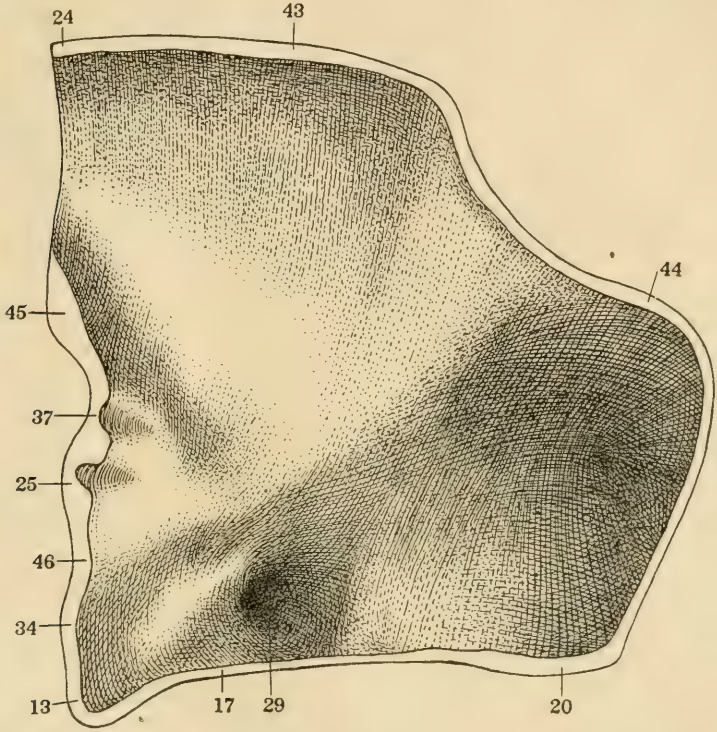

Fig. 8 Mesial view of forebrain reconstruction of 7 mm. cat embryo. × 100. The unshaded area shows the cut surfaces of the reconstruction. *13*, infundibular process; *17*, infundibular region; *20*, lamina terminalis; *24*, mid-brain; *25*, mammillary region; *29*, optic evagination; *34*, post-infundibular eminence; *37*, post-mammillary evagination; *43*, thalamencephalon; *44*, telencephalon; *45*, tuberculum postero-superius; *46*, tubercle of the floor of Schulte.

Cat embryo of 7 mm.; Specimen No. 266 (*fig. 8*). Changes in this embryo have occurred both in the mammillary and infundibular regions. The former now shows a subdivision into what must be considered the mammillary recess (*26*), and dorsal to this a smaller evagination, the post-mammillary recess (*37*). Both of these evaginations affect the median plane, while in the mammillary area two lateral diverticula have appeared, the anlages of the mammillary bodies.

The subsequent history of the post-mammillary evagination shows that this recess is involved in the development of the corpus interpedunculare. In the infundibular region, the optico-infundibular ridge is much less prominent and the entire region is increased in size. Its notable characteristics at this stage are a large infundibular process (*13*) and a prominent post-infundibular eminence (*34*).

The infundibular evagination now contains an extension of the prosencephalic ventricle, in this respect differing from the conditions in the 4.5 mm. embryo in which the infundibular process is solid and as yet contains no ventricular extension.

The optic vesicle (*29*) presents a distinct cupping upon its latero-cephalic surface and is continuous with the lateral wall of the prosencephalon by means of a constricted stem, the optic peduncle (*30*). Along the cephalic surface of this peduncle runs a shallow groove, which becomes expanded as it passes out upon the latero-cephalic surface of the cup. Entally a groove connects the canal of the two optic stems across the floor of the prosencephalon. This is the interoptic groove. Cephalad as well as caudad to this groove the floor is thin. In this stage, therefore, the remodelling of the floor has resulted in the subdivision of the mammillary region, forming the mammillary and post-mammillary evaginations, while laterally the anlages of the mammillary bodies have become defined. The infundibular region likewise shows an advance in its subdivisions, i.e., the infundibular process (*13*) and the post-infundibular eminence (*34*). The rest of the infundibular regions still remains in the general plane of the prosencephalic floor.

Cat embryo of 10 mm.; Specimen No. 498 (*fig. 9*). The changes in this stage are more evident in the telencephalon and thalamencephalon than in the floor-plate. The optic cup is now more pronounced than in the earlier stage, the optic stem still more constricted.

Entally a well marked interoptic groove (*19*) is present, and immediately caudal to this the floor-plate is thickened to form the interoptic torus. The floor of the infundibular region from the torus to the infundibular evagination is thin. The infundib-

ular evagination shows a constriction at its point of junction with the infundibular region, in this way demarcating the definitive infundibular stem (*11*) and the infundibular process (*13*). The ventricular cavity extends through the narrow in-

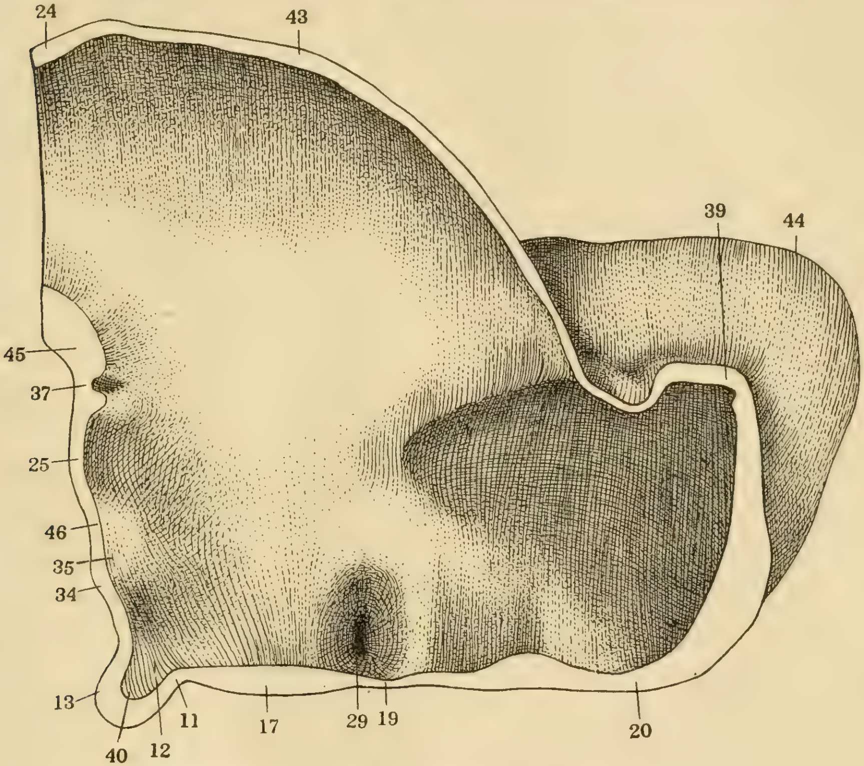

Fig. 9 Mesial view of forebrain reconstruction of 10 mm. cat embryo. × 100. The unshaded area shows the cut surfaces of the reconstruction. *11*, infundibular stem; *12*, infundibular canal; *13*, infundibular process; *17*, infundibular region; *19*, inter-optic groove; *20*, lamina terminalis; *24*, mid-brain; *25*, mammillary region; *29*, optic evagination; *34*, post-infundibular eminence; *35*, post-infundibular recess; *37*, post-mammillary evagination; *39*, paraphysis; *40*, recess of the infundibular process; *43*, thalamencephalon; *44*, telencephalon; *45*, tuberculum postero-superius; *46*, tubercle of the floor of Schulte.

fundibular process, thus giving rise to the infundibular canal (*12*) and the infundibular recess (*40*). Dorsal to the infundibular stem the floor of the ventricle shows a large post-infundibular evagination, which from this time maintains the same general

relation to the infundibular process and for this reason may be designated the post-infundibular eminence (*34*). The cavity of this eminence which communicates with the third ventricle forms the post-infundibular recess (*35*). A slight ridge which is the remnant of the floor tubercle (*46*) (tuberculum postero-inferius) separates the post-infundibular recess from the mammillary evagination (*26*) which, as in the 7 mm. embryo, presents two subdivisions affecting the mid-sagittal plane, i.e., the mammillary and post-mammillary evaginations; while laterally two large diverticula defining the anlages of the mammillary body have increased in prominence but still retain an ample recess, the recessus mammillaris, which is in communication with the third ventricle. Dorsal to the post-mammillary evagination is the tuberculum postero-superius (*45*) now somewhat increased in size.

Cat embryo of 12 mm.; Specimen No. 217 (*fig. 10*). The advance in this embryo over that of 10 mm. appears in the fact that all the definitive elements of the diencephalic floor are now discernible. The most conspicuous changes affect the region of the interoptic groove and the area caudal to it. Where this optic groove formerly appeared as a furrow extending between the orifices of the optic peduncles, the floor is still relatively thin; but caudal to this groove, both entally and ectally, it presents a pronounced thickening, the ectal increase in size being due to the beginning formation of the optic chiasm (*4*), while entally the thickening forms the chiasmatic process (*2*). Thus the furrow in front of the process becomes the prechiasmatic recess (*38*). Ascending from the latter the lamina terminalis (*20*) extends obliquely cephalo-dorsad to join the roof-plate. Quite as notable as the changes which have occurred in the region of the chiasm are those which appear in the area immediately caudad to it. Here the diencephalic floor, without increasing in thickness, presents a ventral protrusion which forms the post-chiasmatic eminence (*32*). This eminence is symmetrically disposed with reference to the mid-sagittal line. Caudal to this is the infundibular stem (*11*) considerably lengthened and expanding to form the infundibular process (*13*). Between the

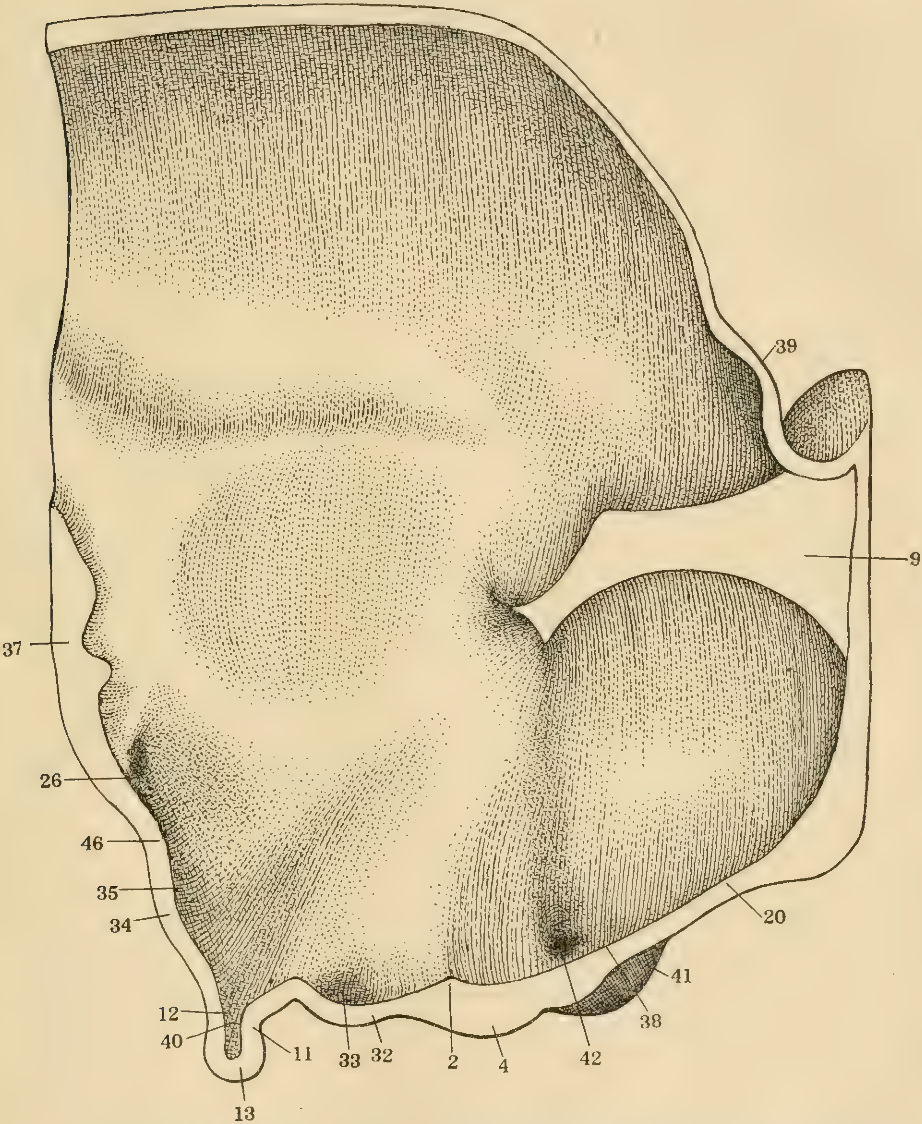

Fig. 10 Mesial view of forebrain reconstruction of 12 mm. cat embryo. × 100. The unshaded area shows the cut surfaces of the reconstruction. *2*, chiasmatic process; *4*, chiasm; *9*, foramen of Monro; *11*, infundibular stem; *12*, infundibular canal; *13*, infundibular process; *20*, lamina terminalis; *26*, mammillary recess; *32*, post-chiasmatic eminence; *33*, post-chiasmatic recess; *34*, post-infundibular eminence; *35*, post-infundibular recess; *37*, post-mammillary evagination; *38*, pre-chiasmatic recess; *41*, supra-optic crest; *42*, supra-optic recess.

infundibular stem and the mammillary evagination (*26*) is a small but distinct diverticulum of the floor appearing as a prominence upon the ectal surface and forming the post-infundibular eminence (*34*).

The mammillary evagination is still large and its cavity spacious. In it may still be recognized the subdivisions already described, i.e., the two lateral evaginations of the mammillary bodies, the median mammillary evagination (*26*) and the post-mammillary evagination (*37*). All of the eminences mentioned have their corresponding recesses, i.e., the post-chiasmatic recess (*33*), the post-infundibular recess (*35*), the mammillary recess (*26*) and the post-mammillary recess. The ventricle extends through a short and narrow infundibular canal (*12*) into a relatively large recess of the infundibular process.

The eye-cup in this stage is now completely formed. It is attached to the prosencephalon by the optic peduncle; but certain changes have occurred in this peduncle which have important bearings upon the structures evolved from it. As the peduncle approaches the brain-wall it becomes rapidly expanded in the form of a distinct evagination of the prosencephalon, into which extends an expansion of the ventricle. Ventral to this evagination the optic peduncle has increased in thickness, due to the appearance of fibers forming the optic nerve and entering the optic chiasm (*4*). In this manner a diverticulum of the third ventricle comes to overlie the lateral portion of the optic chiasm and the proximal portion of the optic nerve. This diverticulum is the supraoptic recess (*42*).

Cat embryo of 15 mm.; Specimen No. 505 (*fig. 11*). In this embryo a foreshortening has occurred in the diencephalic floor. This is due principally to the change in the inclination of the lamina terminalis (*20*) which is now vertical. In consequence of this alteration the prechiasmatic recess has become the most cephalic portion of the ventricle. The chiasmatic process (*2*) and the chiasm have increased in size. The post-chiasmatic eminence is still further expanded and its recess is larger. The post-infundibular eminence (*34*) occupies a typical position between the infundibular stem (*11*) and the mammillary evagi-

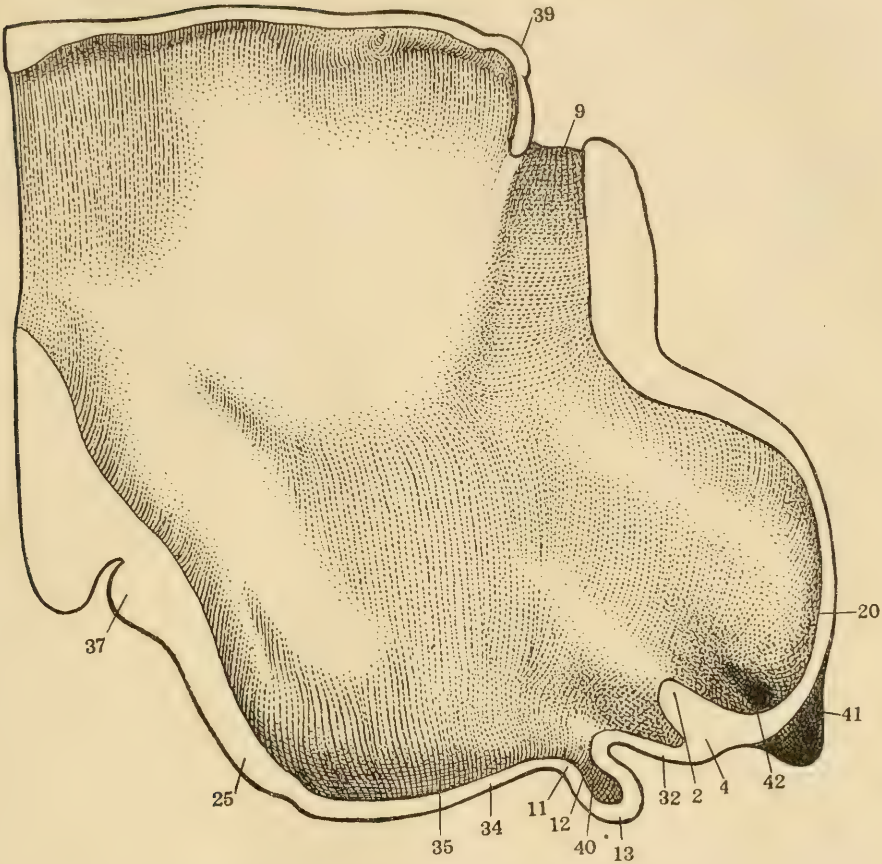

Fig. 11 Mesial view of forebrain reconstruction of 15 mm. cat embryo × 75. The unshaded area shows the cut surfaces of the reconstruction. *2*, chiasmatic process; *4*, chiasm; *11*, infundibular stem; *12*, infundibular canal; *13*, infundibular process; *20*, lamina terminalis; *25*, mammillary region; *32*, post-chiasmatic eminence; *34*, post-infundibular eminence; *35*, post-infundibular recess; *37*, post-mammillary evagination; *40*, recess of infundibular process; *41*, supra-optic crest; *42*, supra-optic recess.

nation (*26*). In this latter evagination is possible to recognize a median, a post-mammillary and two lateral recesses. The infundibular stem has increased in length so that the infundibular canal (*12*) is longer, while the infundibular process shows a distinct thickening along its ventro-cephalic surface, thus

giving evidence that the growth going on in this structure at this stage is in a cephalic direction. The optic peduncle has increased in size, due to the addition of more optic fibers.

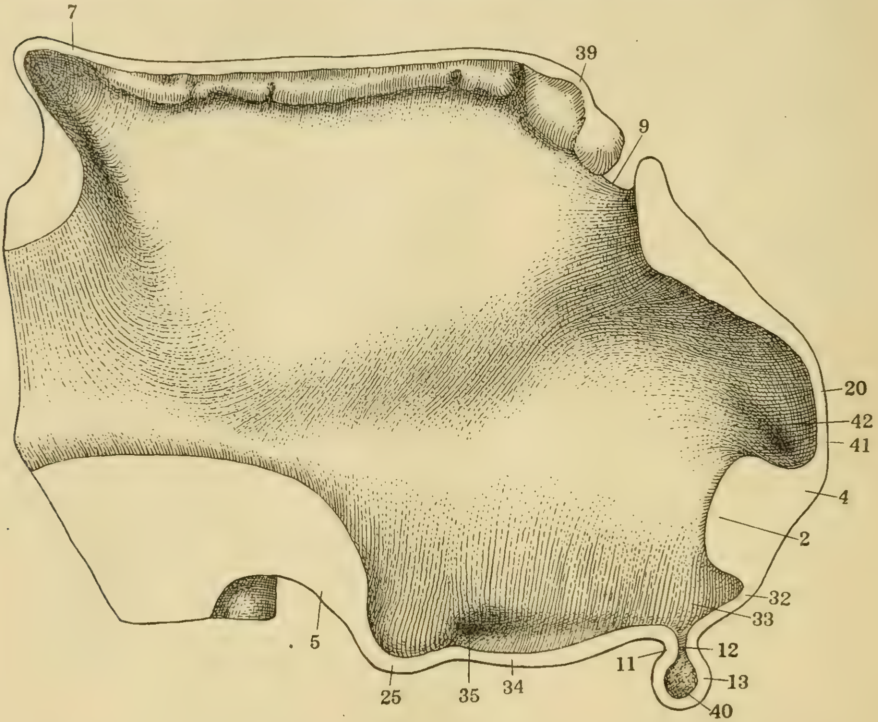

Fig. 12 Mesial view of forebrain reconstruction of 30 mm. cat embryo. × 50. The unshaded area shows the cut surfaces of the reconstruction. *2*, chiasmatic process; *4*, chiasm; *5*, corpus interpedunculare; *7*, epiphysis; *9*, foramen of Monro; *11*, infundibular stem; *12*, infundibular canal; *13*, infundibular process; *20*, lamina terminalis; *25*, mammillary region; *32*, post-chiasmatic eminence; *33*, post-chiasmatic recess; *34*, post-infundibular eminence; *35*, post-infundibular recess; *39*, paraphysis; *40*, recess of the infundibular process; *41*, supra-optic crest; *42*, supra-optic recess.

Cat embryo of 30 mm.; Specimen No. 585 (*fig. 12*). The foreshortening of the diencephalic floor observed in the embryo of 15 mm. is here less pronounced, although the lamina terminalis (*20*) retains its vertical position. The prechiasmatic and supra-optic recesses are more pronounced, due to the increase in size of the chiasmatic process (*2*). The chiasmatic fibers are present in large numbers in the ventral aspect, while the dorsal extension

of the chiasmatic process appears to be due to the presence of increasing numbers of commissural fibers. The post-chiasmatic eminence (*32*) has increased in size, both in the median line as well as laterally, where it now begins to present free extremities. Its recess is deep and projects cephalad under the chiasmatic process in such a way that coronal sections of the brain in this stage show a distinct recess which extends forward beneath the chiasmatic process. The infundibular stem and the infundibular process have both increased in size; the tendency of the latter to extend its growth cephalad has about ceased, and the entire infundibular process seems to be on the point of swinging dorso-caudad in its further development. The general shape of the process at this stage is oval, and the two relatively long lateral processes appear on either side. The infundibular canal (*12*) is relatively longer and the recess of the infundibular process not only more spacious but more definitely demarcated from the canal than in any earlier stage.

Caudad to the infundibular stem (*11*) is a large post-infundibular eminence (*34*) containing a well defined post-infundibular recess (*35*), which latter is separated by a transverse ridge from the mammillary recess. The neural wall bounding this recess and thus forming the mammillary eminence (*27*) has notably increased in thickness, so that the relative dimensions of the diencephalic ventricle are being lessened by the encroachment due to the thickening of the brain floor in the region of the mammillary bodies. This thickening particularly affects the two lateral mammillary diverticula, while the median mammillary and post-mammillary evaginations are no longer discernible. Thickening has also occurred in the region of the post-mammillary evagination, and this area now shows an ectal protuberance marking the site of the corpus interpedunculare (*5*).

Cat embryo of 51 mm.; Specimen No. 104 (fig. 13). The changes observed in this stage involve the further development of the chief tendencies observed in the 30 mm. embryo, i.e., the pronounced caudal deflection of the infundibular process (*13*) which appears as a distinct appendage to the floor of the ventricle, due to the increased length and constriction of the infundibular stem (*11*). This process now presents two surfaces, one which faces

cephalad and is relatively thick and the other which faces caudad and is thin. Both of these surfaces are closely invested by the pars infundibularis of the pituitary gland and their continuation laterad produces two long and slender lateral processes. The

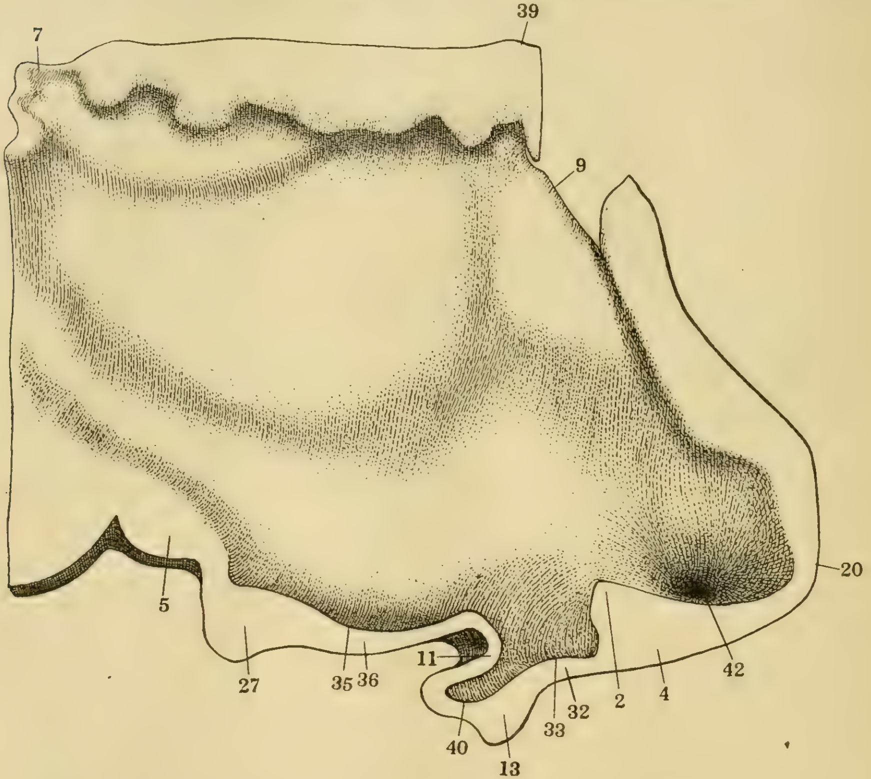

Fig. 13 Mesial view of forebrain reconstruction of 51 mm. cat embryo. × 50. The unshaded area shows the cut surfaces of the reconstruction. *2*, chiasmatic process; *4*, chiasm; *5*, corpus interpedunculare; *7*, epiphysis; *9*, foramen of Monro; *11*, infundibular stem; *13*, infundibular process; *20*, lamina terminalis; *27*, mammillary body; *32*, post-chiasmatic eminence; *33*, post-chiasmatic recess; *35*, post-infundibular recess; *36*, post-infundibular evagination; *39*, paraphysis; *40*, recess of the infundibular process; *42*, supra-optic recess.

brain floor in the mammillary region is still further increased in thickness and two definite lateral protuberances, one on either side of the median line, have made their appearance. Because of the increased thickness of the neural tissue which bounds them the lateral diverticula of the mammillary recess have

greatly decreased in size and seem to be on the point of disappearing.

The median mammillary and post-mammillary evaginations are no longer recognizable, but a protuberance marking the position of the corpus interpedunculare (*5*) is still defined as the

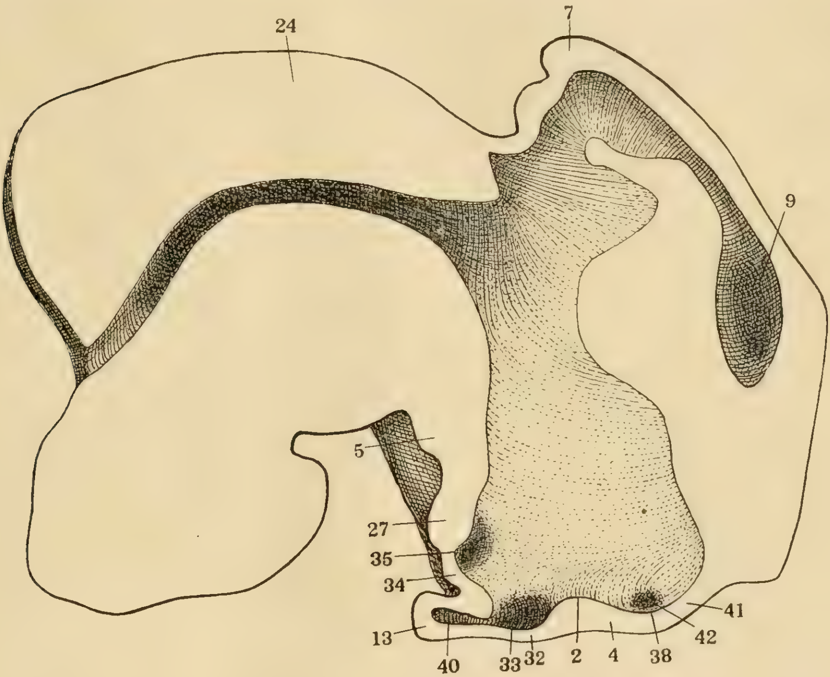

Fig. 14 Mesial view of forebrain reconstruction of 70 mm. cat embryo. × 25. The unshaded area shows the cut surface of the reconstruction. *2*, chiasmatic process; *4*, chiasm; *5*, corpus interpedunculare; *13*, infundibular process; *27*, mammillary body; *32*, post-chiasmatic eminence; *33*, post-chiasmatic recess; *34*, post-infundibular eminence; *35*, post-infundibular recess; *38*, pre-chiasmatic recess; *40*, recess of infundibular process; *41*, supra-optic crest; *42*, supra-optic recess.

thickened area in that part of the floor. The other eminences and recesses defined in the earlier stages are all present with but slight changes.

Cat embryo of 70 mm.; Specimen No. E 70 (fig. 14). In its main outlines the diencephalic floor at this stage has attained its adult conformation. It is not, however, disposed in the

ultimate plane of the floor as yet, for the region of the post-infundibular and mammillary areas has assumed a more vertical position than is true of the 15, 30 and 51 mm. stages and this position will later be so modified in attaining adult conditions that the most dorsal element in this region, the corpus interpedunculare (*5*), will be rotated ventrad through an arc of nearly 90°. All of the eminences observed in the early stages and their corresponding recesses are here present. The infundibular process (*13*) presents two well marked, lateral processes, one on either side; the post-chiasmatic eminence (*32*) likewise presents two lateral processes which project free beneath the suprajacent lateral eminences of the tuber cinereum. The wall of the post-infundibular eminence (*34*) has increased in thickness and it bounds a spacious post-infundibular recess (*35*). Two mammillary bodies are now present, but the mammillary recess (*26*) cannot be defined because of the thickening which has progressed in the development of the mammillary region. The corpus interpedunculare (*5*) forms the most dorsal element in this portion of the ventricular floor; the prechiasmatic and supraoptic recesses (*38* and *42*), the latter extending out upon the optic nerve for some distance, are both present.

Development of the diencephalic floor in the chick

Chick of twenty-three hours; eight somites; Specimen No. 618 (*fig. 15*). The forebrain at this stage consists exclusively of the large optic vesicles similar in all respects to the vesicles in the cat, although their transverse diameter is greater and their altitude less. Entally the horizontal segment of the optic sulcus is well defined, extending from the deepest portion of the optic evagination (*29*) obliquely meso-caudad and converging with the corresponding sulcus of the opposite side. The angle formed by the convergence of these two sulci is occupied by a clearly defined prominence, the tubercle of the floor (*46*). The neuropore (*28*) is still open for a considerable distance at the cephalic extremity of neural folds, but its closure is more advanced than in the cat embryo of eight somites.

Chick of forty-nine hours; twenty somites; Specimen No. 619 (*fig. 16*). The advances in this stage consist in the reduction

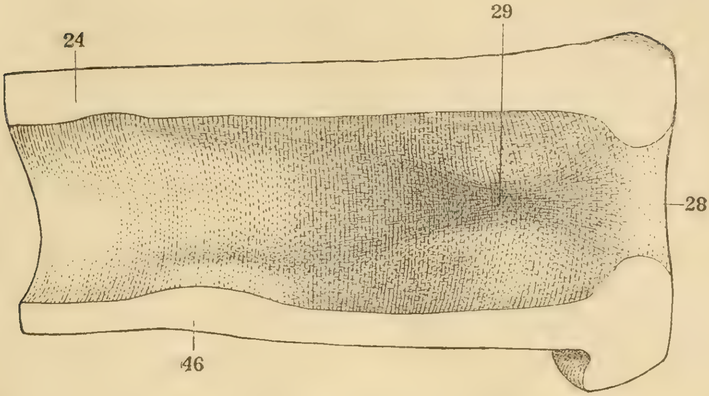

Fig. 15 Mesial view of forebrain reconstruction of 8 somite chick. × 150. The unshaded area shows the cut surfaces of the reconstruction. *24*, mid-brain; *28*, neuropore; *29*, optic evagination; *46*, tubercle of the floor of Schulte.

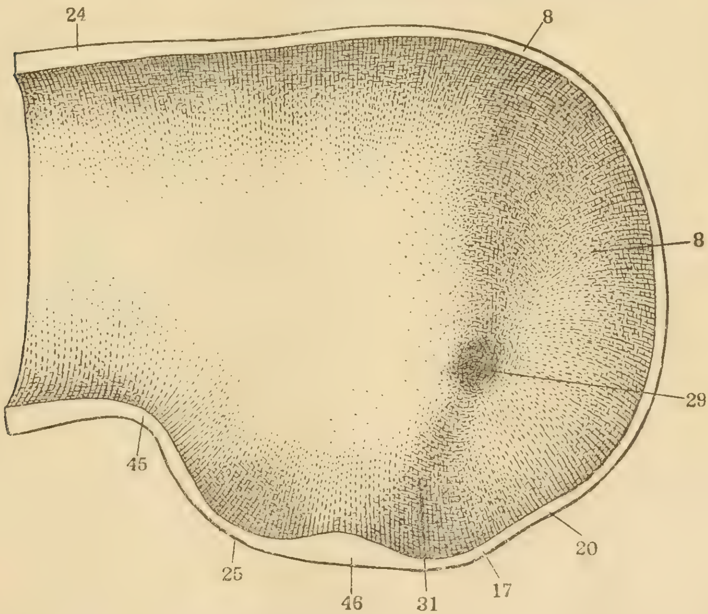

Fig. 16 Mesial view of forebrain reconstruction of 20 somite chick. × 150. The unshaded area shows the cut surfaces of the reconstruction. *8*, ectoptic zone of Schulte; *17*, infundibular region; *20*, lamina terminalis; *24*, mid-brain; *25*, mammillary region; *29*, optic evagination; *31*, optico-infundibular groove; *46*, tubercle of the floor of Schulte.

of the primitive optic vesicles (*29*) and the formation of the ectoptic zone (*8*) which now presents its dorsal, cephalic and ventral segments. Further advance is found in the formation of a definite mammillary region (*25*). The boundary between midbrain and forebrain is indicated by the tuberculum postero-superius (*45*). The ventral segment of the ectoptic zone appears as a well defined infundibular region (*17*) and a wide, shallow groove extends from the orifice of the optic evagination to the apex of this region, forming the optico-infundibular groove (*31*). A slight transverse ridge separates the mammillary and infundibular regions thus marking the position of the tubercle of the floor

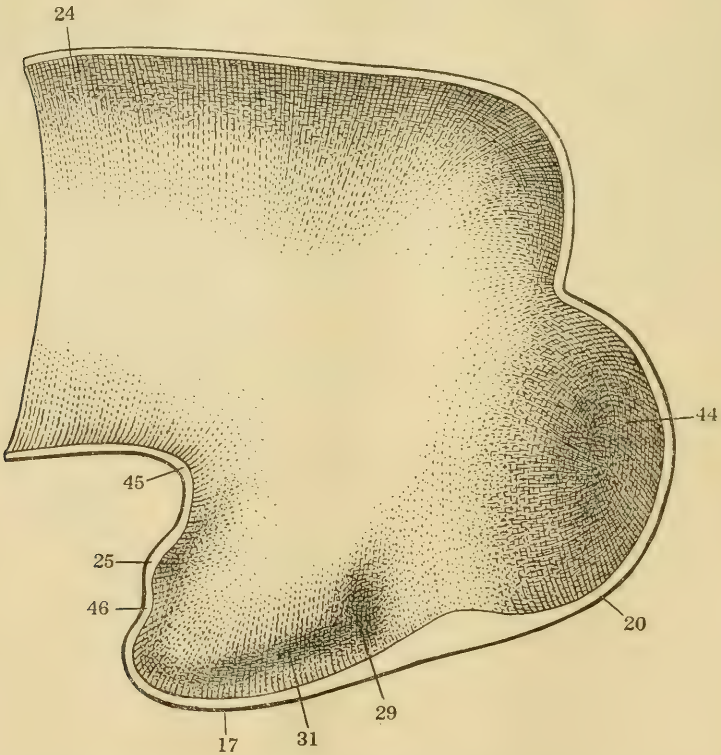

Fig. 17 Mesial view of forebrain reconstruction of 6.75 mm. chick. × 150. *17*, infundibular region; *20*, lamina terminalis; *24*, mid-brain; *25*, mammillary region; *29*, optic vesicle or evagination; *31*, optico infundibular groove; *44*, telencephalon; *45*, tuberculum postero-superius; *46*, tubercle of the floor of Schulte.

(*46*). Ectally the mammillary and infundibular regions present distinct eminences.

Chick of 108 hours; 6.75 mm.; Specimen No. 371 (*fig. 17*). The tendency of the infundibular region (*17*) to assume a more ventral relation with reference to the mammillary region is here more pronounced. Otherwise, with the exception of the greater

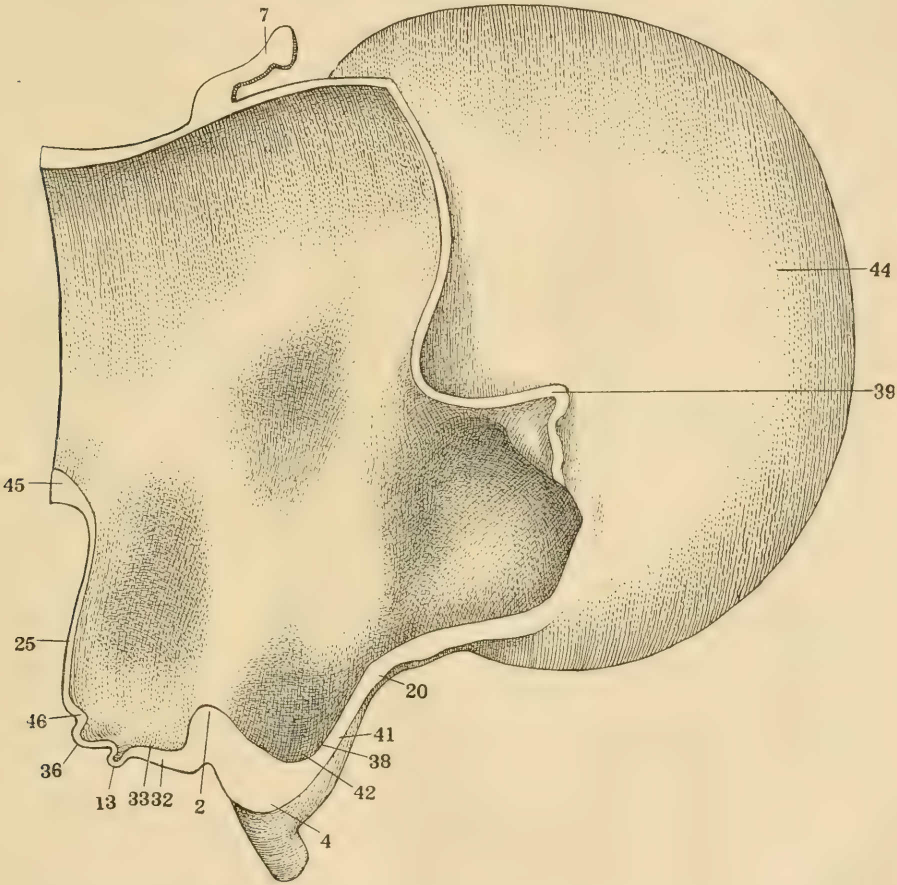

Fig. 18 Mesial view of forebrain reconstruction of chick of 5 days and 20 hours. × 100. The unshaded area shows the cut surfaces of the reconstruction. *2*, chiasmatic process; *4*, chiasm; *7*, epiphysis; *13*, infundibular process; *20*, lamina terminalis; *25*, mammillary region; *32*, post-chiasmatic eminence; *33*, post-chiasmatic recess; *36*, post-infundibular eminence; *38*, pre-optic recess; *39*, paraphysis; *41*, supra-optic crest; *42*, supra-optic recess; *44*, telencephalon; *45*, tuberculum postero-superius; *46*, tubercle of the floor of Schulte.

reduction of the optic vesicles, there are no notable changes in this stage.

Chick of five days, twenty hours; Specimen No. 326 (fig. 18). In this stage a marked change has occurred in the infundibular region (*17*) namely, the appearance of two distinct evaginations at the apex of this region, the more ventral of which is involved in the formation of the infundibular process (*13*), while the more dorsal one ultimately forms the post-infundibular eminence (*34*). These two evaginations of the infundibular region are more pronounced in the chick than in either the cat or the dog-fish. The mammillary region (*25*) has increased in size, but occupies a position dorsal to the infundibular region as in the immediately preceding stage. The mammillary recess (*26*) is correspondingly larger. Thus the floor of the third ventricle now presents three separate evaginations, the infundibular evagination (*18*), the post-infundibular evagination (*36*) and the mammillary evagination (*26*), a condition corresponding in all details to the early history of the development in the mammillary and infundibular regions of the cat. At this stage also a large chiasmatic process (*2*) has appeared thus demarcating a prechiasmatic recess (*38*) and a post-chiasmatic recess (*33*). This latter recess is marked upon the exterior surface by a prominent post-chiasmatic eminence (*32*).

Chick of eight days; Specimen No. 315 (fig. 19). In this stage all of the definitive elements of the diencephalic floor are present. The chiasm (*4*) and the chiasmatic process (*2*) have increased in size with the consequence that the prechiasmatic and post-chiasmatic recesses (*38* and *33*) are more pronounced. The supraoptic crest (*41*) and supraoptic recess (*42*) are both present. The post-chiasmatic eminence (*32*) has also increased in prominence. It now shows a distinct longitudinal furrow which marks the inception of the median post-chiasmatic groove. In the region of this groove the floor is relatively thin, while upon either side of it the neural tissue has a considerable thickness. In the caudal portion of the infundibular region the dorsal and ventral evaginations are more marked than in the next earlier stage and in them may be distinguished the anlages of the infundibular process (*13*) and post-infundibular eminence (*34*).

The infundibular process manifests a tendency toward the development of a short infundibular stem (*11*) while at the sides it gives the first evidence of its lateral processes (*16*). The mammillary region presents two large lateral processes and a smaller median recess with surface markings corresponding with these evaginations. The mammillary recess (*26*) as a whole is gradually being reduced, due to a thickening of its lateral walls.

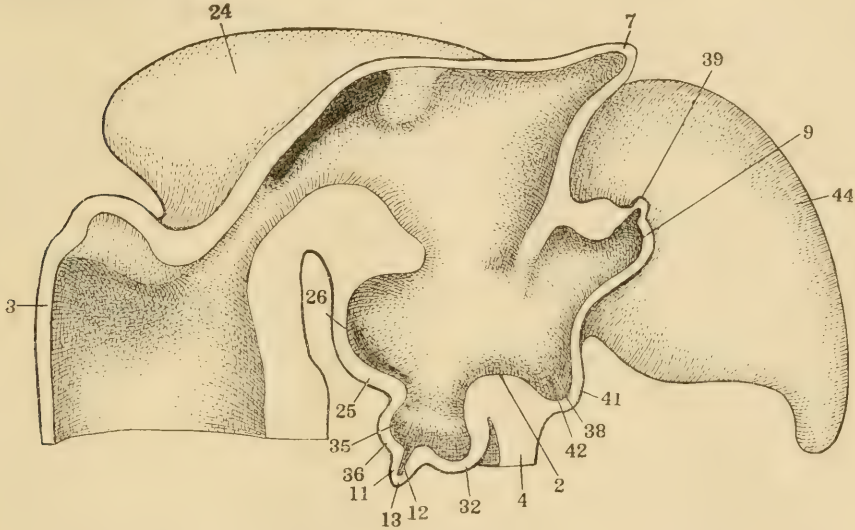

Fig. 19 Mesial view of forebrain reconstruction of chick of 8 days. × 50. The unshaded area shows the cut surfaces of the reconstruction. *2*, chiasmatic process; *3*, cerebellum; *4*, chiasm; *7*, epiphysis; *9*, foramen of Monro; *11*, infundibular stem; *12*, infundibular canal; *13*, infundibular process; *16*, infundibular process (lateral process); *24*, mid-brain; *25*, mammillary region; *26*, mammillary recess; *32*, post-chiasmatic eminence; *36*, post-infundibular eminence; *38*, pre-chiasmatic recess; *41*, supra-optic crest; *42*, supra-optic recess; *44*, telencephalon.

Chick of nine days, nineteen hours; Specimen No. 919 (*fig. 20*). The reconstruction of this stage shows no material change in the supraoptic crest (*41*), supraoptic and prechiasmatic recesses (*42* and *38*). The chiasmatic process (*2*) is less prominent than in the eight-day chick, although the chiasm (*4*) has increased relatively in size. Caudal to the chiasm the post-chiasmatic eminence (*32*) has gained somewhat in prominence. It now

shows clearly the median post-chiasmatic groove and the two lateral processes, one on either side of this groove. More marked is the change in the caudal portion of the infundibular region where the infundibular process is now well formed, and connected with the floor of the diencephalon by a short, broad stalk, the infundibular stem *(11)*. The infundibular process itself

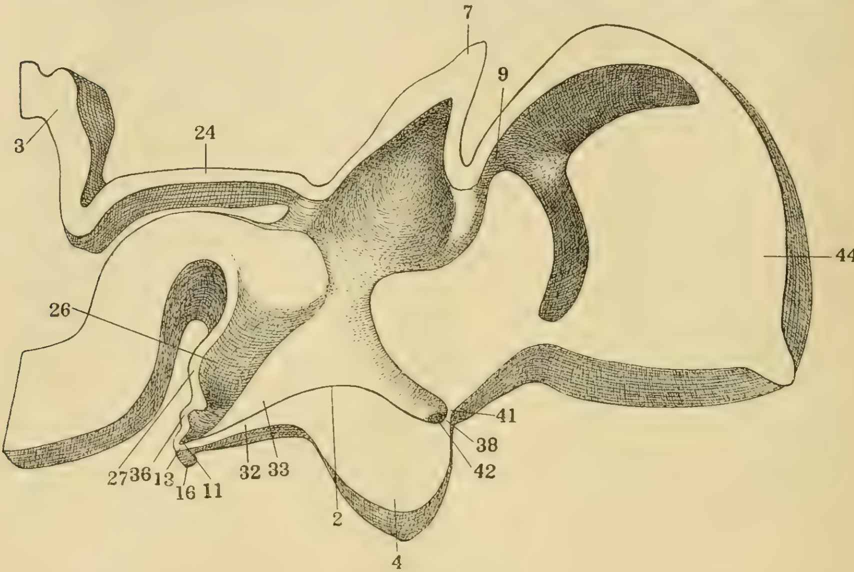

Fig. 20 Mesial view of forebrain reconstruction of chick of 9 days and 19 hours. × 50. The unshaded area shows the cut surfaces of the reconstruction. *2*, chiasmatic process; *3*, cerebellum; *4*, chiasm; *7*, epiphysis; *9*, foramen of Monro; *11*, infundibular stem; *13*, infundibular process; *24*, mid-brain; *26*, mammillary recess; *27*, mammillary body; *32*, post-chiasmatic eminence; *33*, post-chiasmatic recess; *36*, post-infundibular eminence; *38*, pre-chiasmatic eminence; *41*, supra-optic crest; *42*, supra-optic recess; *44*, telencephalon.

presents a median expanded portion, from which there extends to either side a slender lateral process. This formation corresponds closely to the conditions in the infundibular process of Mustelus at the stage of 50 mm. The ventricular cavity extends through the infundibular stem and upon entering the infundibular process rapidly expands into a number of branching diverticula. These diverticula are confined largely to the dorsal surface of the infundibular process and extend from its median

portion into the lateral processes. At this stage, therefore, it is possible to distinguish between a dorsal or saccular surface and a ventral surface, the latter being in contact with the anlage of the pituitary gland.

Dorsal to the stem of the infundibular process is a small evagination corresponding in its general relations to the part already described as the anlage of the post-infundibular eminence (*36*). Its growth has been less pronounced than that of the other parts of the infundibular region. The cavity of the third ventricle extends into it forming the post-infundibular recess (*35*). In the mammillary region (*25*) the tendency toward the reduction of the ventricular cavity already noted in the chick of eight days has proceeded still further. The mammillary region itself forms a large protuberance dorsal to the post-infundibular eminence. The lateral median evaginations are still prominent on the surface, but the cavities contained in them have been greatly reduced now forming small accessory recesses connected with the third ventricle. The median mammillary recess (*26*) is still prominent sagittally, although its transverse diameters are much reduced. The mammillary bodies are now defined upon the surface.

Chick of fourteen days, eighteen hours; Specimen No. 1418 (fig. 21). In this stage adult conditions have practically been attained. The post-chiasmatic eminence (*32*) is less prominent with the result that the prechiasmatic recess (*38*) is less well defined. Traced laterad, however, this recess may be followed into a small canal overlying the chiasm and proximal portion of the optic nerve, the supraoptic recess (*42*). The position of this recess is marked upon the surface by the supraoptic crest (*41*). In the infundibular region the post-chiasmatic eminence is well defined; its median post-chiasmatic groove (*23*) as well as its two lateral processes are prominent. The caudal portion of the infundibular region shows but little change. The main portion of the infundibular process is somewhat larger; its dorsal convoluted surface is in even greater contrast to the ventral pituitary surface because of its more marked convolution. The third ventricle communicates with the infundibular process

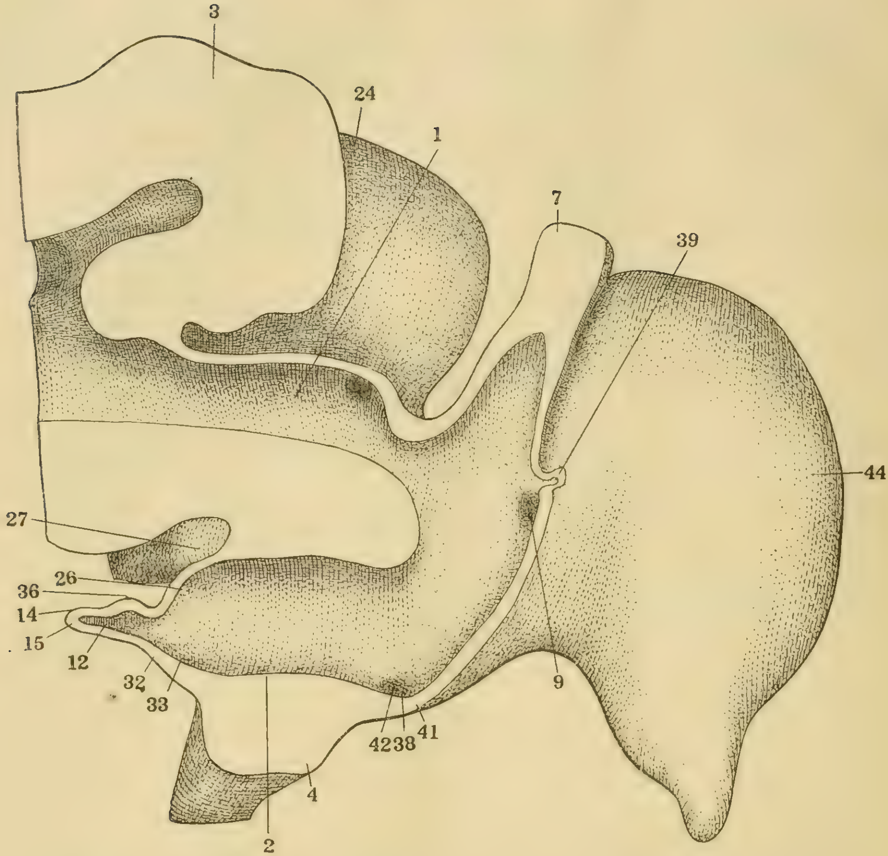

Fig. 21 Mesial view of forebrain reconstruction of 14 days and 18 hours chick. × 25. *1*, aqueduct of Sylvius; *2*, chiasmatic process; *3*, cerebellum; *4*, optic chiasm; *7*, epiphysis; *9*, foramen of Monro; *12*, infundibular canal; *14*, infundibular process, saccular surface; *15*, infundibular process, pituitary surface; *24*, mid-brain; *26*, mammillary recess; *27*, mammillary body; *32*, post-chiasmatic eminence; *33*, post-chiasmatic recess; *36*, post-infundibular eminence; *38*, pre-chiasmatic recess; *39*, paraphysis; *41*, supra-optic groove; *42*, supra-optic recess; *44*, telencephalon.

by an extremely small canal, while the infundibular recess presents many branching subdivisions which extend to the several diverticula of the dorsal convoluted surface. The post-infundibular eminence occupies its characteristic position and has not changed in size. It still retains the post-infundibular recess of the ventricle.

In the mammillary region the processes initiated in the stage of eight days have now proceeded to such a degree that the lateral mammillary recesses have become obliterated and the mammillary bodies are now solid, containing no recess accessory to the third ventricle. There is still a slight remnant of the median mammillary recess (*26*), but this also has been considerably reduced in size.

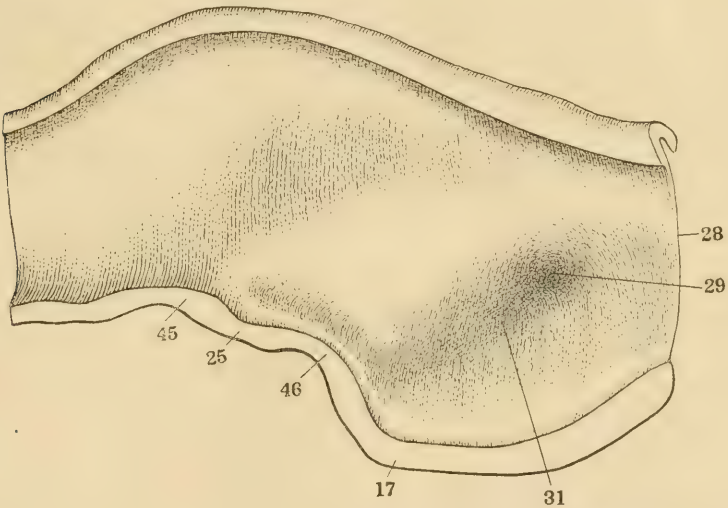

Fig. 22 Mesial view of forebrain reconstruction of 3 mm. Mustelus laevis. × 150. The unshaded area shows the cut surfaces of the reconstruction. *17*, infundibular region; *25*, mammillary region; *28*, neuropore; *29*, optic vesicle or evagination; *31*, optico-infundibular groove; *45*, tuberculum postero-superius; *46*, tubercle of the floor of Schulte.

Development of the diencephalic floor in Mustelus laevis

Mustelus embryo of 3 mm.; Specimen No. 722 (fig. 22). The embryo of this stage corresponds closely to the cat embryo of eight somites and is also similar to the chick embryo of that size. The neuropore (*28*) is still widely open, while the optic vesicle (*29*) forms the only structure at the cephalic extremity of the neural tube. Ectally this vesicle is represented by a marked lateral protuberance of the neural wall whose axis is oblique and whose apex is directed caudad. The surface relief of the brain at this stage is shown in figure 23. Dorsal to the

apex of the optic vesicle is a shallow groove which traverses the tube transversely and demarcates the vesicle from a prominent eminence, the mammillary region (*25*). The ental surface of this model (fig. 22) shows the optic vesicle as a shallow evagination from the deepest portion of which a sulcus may be traced ventrad and caudad to the tubercle of the floor (*46*). This is the optic sulcus. The ectoptic zone has not yet made its appearance. The mammillary region is well defined both as an ectal protuberance and an ental recess. The prosencephalon thus presents the two primitive constituents which are characteristic of this period in the cat and chick.

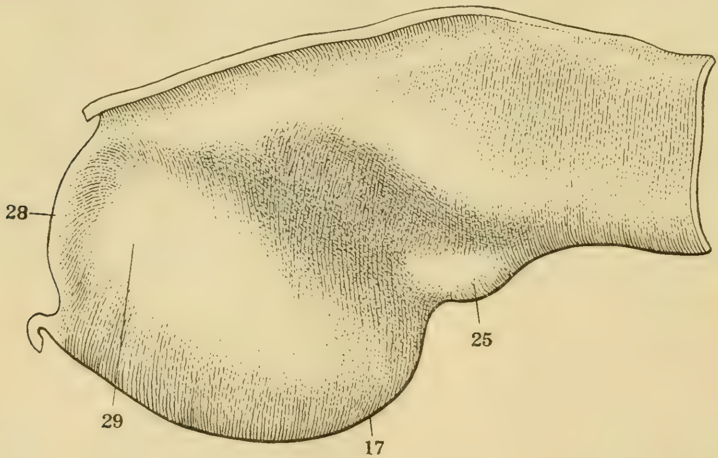

Fig. 23 Ectal view of forebrain shown in figure 22. × 150. The unshaded area shows the cut surfaces of the reconstruction. *17*, infundibular region; *25*, mammillary region; *28*, neuropore; *29*, optic evagination.

Mustelus embryo of 7 mm.; Specimen No. 294 (fig. 24). In this embryo the neuropore is still open, while the advance in development is indicated by the marked reduction of the optic vesicle (*29*) and the appearance of an ectoptic zone (*8*) presenting the three characteristic segments. The dorsal and cephalic segments present respectively the anlages of the thalamencephalon (*43*) and telencephalon (*44*), while the ventral segment now appears in the form of a definite infundibular region (*17*). The reduction of the optic vesicle has been carried to such a degree that the optic cup and optic peduncle may both be dis-

tinguished, the former manifesting as yet but slight cupping, the latter a definitely constricted stem attaching to the lateral wall of the forebrain. The prosencephalic ventricle extends through the optic peduncle into the spacious recess of the eye-cup. The vertical segment of the optic sulcus is not present,

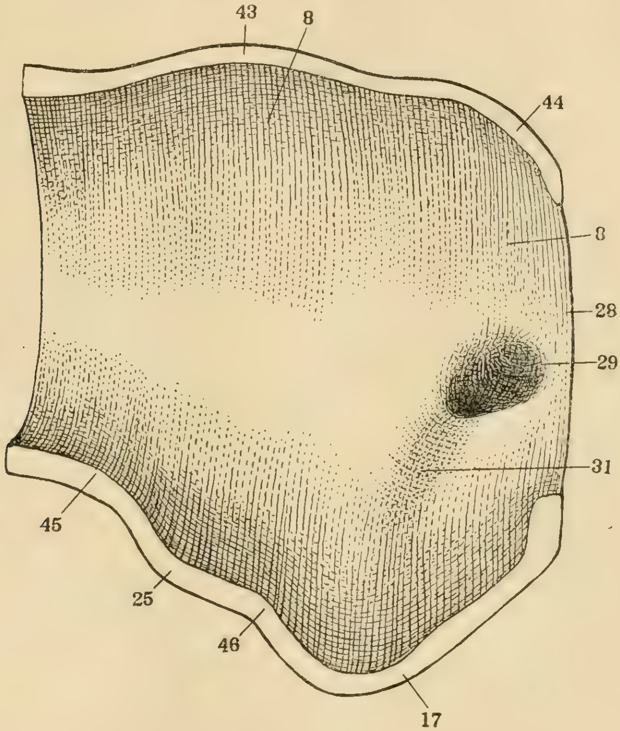

Fig. 24 Mesial view of forebrain reconstruction of 7 mm. Mustelus laevis. × 150. The unshaded area shows the cut surfaces of the reconstruction. *8*, ectoptic zone of Schulte; *17*, infundibular region; *25*, mammillary region; *28*, neuropore; *29*, optic evagination; *31*, optico-infundibular groove; *43*, thalamencephalon; *44*, telencephalon; *46*, tubercle of the floor of Schulte.

but the optico-infundibular groove (*31*) passes in the position of the horizontal segment of the sulcus from the orifice of the optic peduncle (*29*) ventro-caudally to the side of the floor tubercle (*46*). The infundibular and mammillary regions present little change in size. The tuberculum postero-superius (*45*) is not prominent.

Mustelus embryo of 11 mm.; Specimen No. 729 (fig. 25). The midbrain flexures are present in this embryo and have caused deflections of the neural axis at the anterior and at the posterior isthmian sulci. The ectoptic zone now gives more definite evidence of its ultimate derivatives, the dorsal segment showing

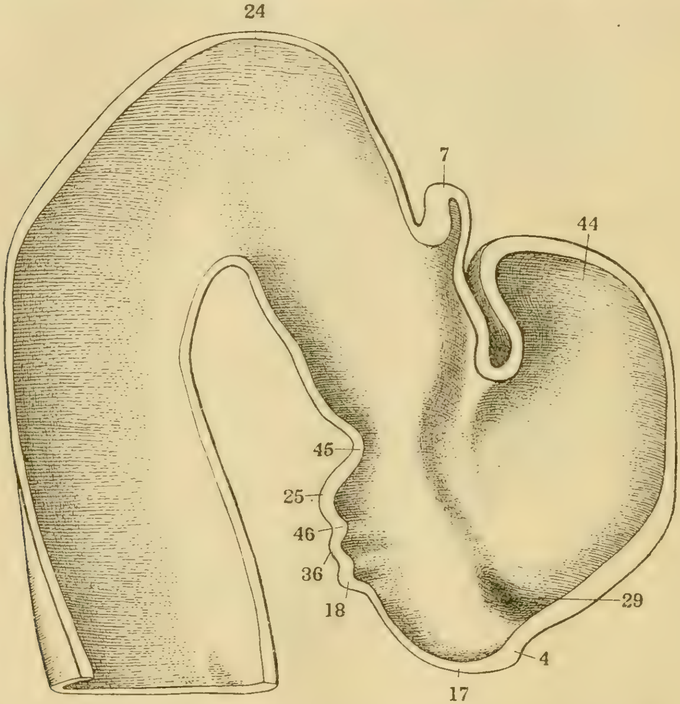

Fig. 25 Mesial view of forebrain reconstruction of 11 mm. Mustelus embryo. × 100. The unshaded area shows the cut surfaces of the reconstruction. *4*, chiasm; *7*, epiphysis; *18*, infundibular evagination; *24*, mid-brain; *25*, mammillary region; *29*, optic evagination; *36*, post-infundibular evagination; *45*, tuberculum postero-superius; *46*, tubercle of the floor of Schulte.

the characteristic thalamencephalic formation, while the cephalic segment presents all of the primitive elements of the telencephalon. The ventral segment of the ectoptic zone is considerably modified. The infundibular region (*17*) has not only increased in size, but at its apex or caudal portion two evaginations have made their appearance. Of these the infundibular evagination (*18*) is more extensive but less protuberant. The pituitary anlage is

in contact with the ectal surface of this evagination, except for a small area immediately ventrad to the dorsal evagination. In these respects the development of Mustelus corresponds in all details to that of the cat and of the chick. The post-infundibular evagination (*36*) is the smaller of these secondary protuberances. Upon its ventricular surface it is demarcated from the mammillary region by a distinct elevation, the tubercle of the floor (*46*). Ventrally it becomes continuous with the ventral infundibular evagination (*18*).

The mammillary region (*25*) has attained a sharper outline without appreciable increase in size. It is assuming the characteristics which lead to the recognition of it as the posterior lobe. The optic vesicle is relatively smaller than the forebrain; its peduncle (*30*) has become more constricted except at its proximal extremity where it presents a slight dilatation into which extends a recess accessory to the ventricle. The optic peduncle still retains its canal which communicates with the residual lumen of the optic cup. The optico-infundibular groove is less well defined than in the earlier stages.

Mustelus embryo of 20 mm.; Specimen No. 730 (figs. 26). In this embryo the anterior and posterior isthmian flexures are present and well marked. All of the elements described in the 11 mm. embryo may be recognized and are but little changed. The principal advances are seen in the thalamencephalon and telencephalon. In the infundibular region, however, a process of importance has been initiated and has already assumed considerable proportions. During the earlier stages it has been in the apex or caudal portion of this region that notable changes were observed. Now and for some time to follow the development of its cephalic portion becomes more conspicuous and salient. Following the ventral border of the optic peduncle, some optic fibers have already made their way inward to form the chiasm (*4*); the floor of the ventricle at the same time has been slightly elevated above the chiasm as a transverse ridge passing between the orifices of the optic peduncles. This ridge, the chiasmatic process (*2*), separates the prechiasmatic and post-chiasmatic recesses. Of these the latter is the more prominent

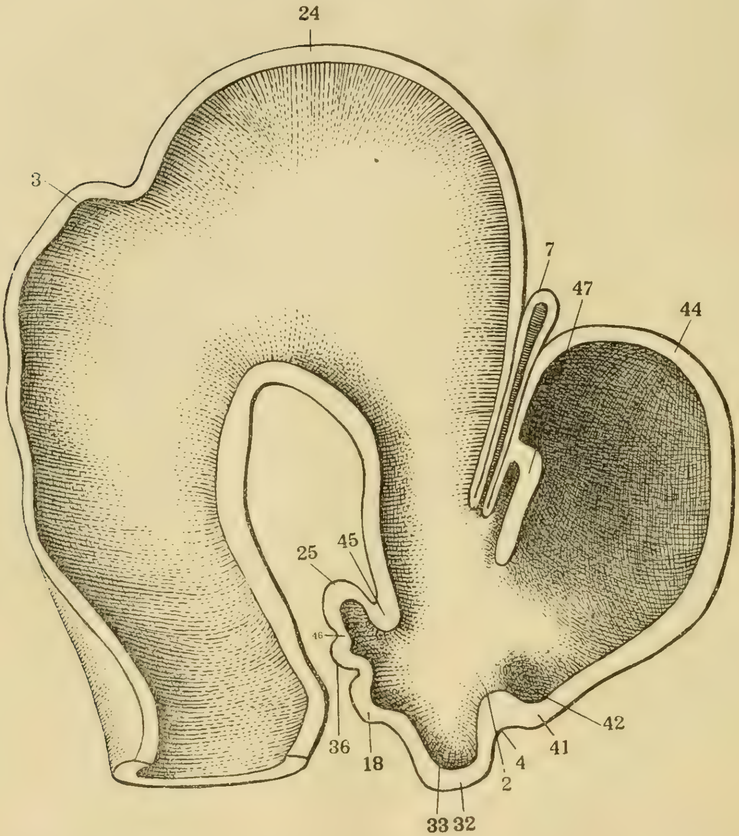

Fig. 26 Mesial view of forebrain reconstruction of 20 mm. Mustelus. × 75. The unshaded area shows the cut surfaces of the reconstruction. *2*, chiasmatic process; *3*, cerebellum; *4*, chiasm; *7*, epiphysis; *18*, infundibular evagination; *24*, mid-brain; *25*, mammillary region; *32*, post-chiasmatic eminence; *33*, post-chiasmatic recess; *36*, post-infundibular eminence; *41*, supra-optic crest; *42*, supra-optic recess; *44*, telencephalon; *46*, tubercle of the floor of Schulte; *47*, velum transversum.

and has expression upon the surface in a large protuberance caudal to the chiasm, the post-chiasmatic eminence. This eminence already shows a demarcation into a shallow post-chiasmatic groove in which the ventricular floor is thin and two large, thick-walled protuberances, the lateral processes of the post-chiasmatic eminence or inferior lobes. The cavity of the

ventricle extends from the narrow median portion of the post-chiasmatic eminence into the two lateral processes, thus forming the recessus lobi inferioris. From the dorsal region of the pituitary anlage two sprouts, each as yet independent of the other, are growing forward along the ventral surface of the median post-chiasmatic groove.

Mustelus of 50 and 70 mm.; Specimens Nos. 725 and 735 (figs. 27 and 28). The development in these stages has carried the differ-

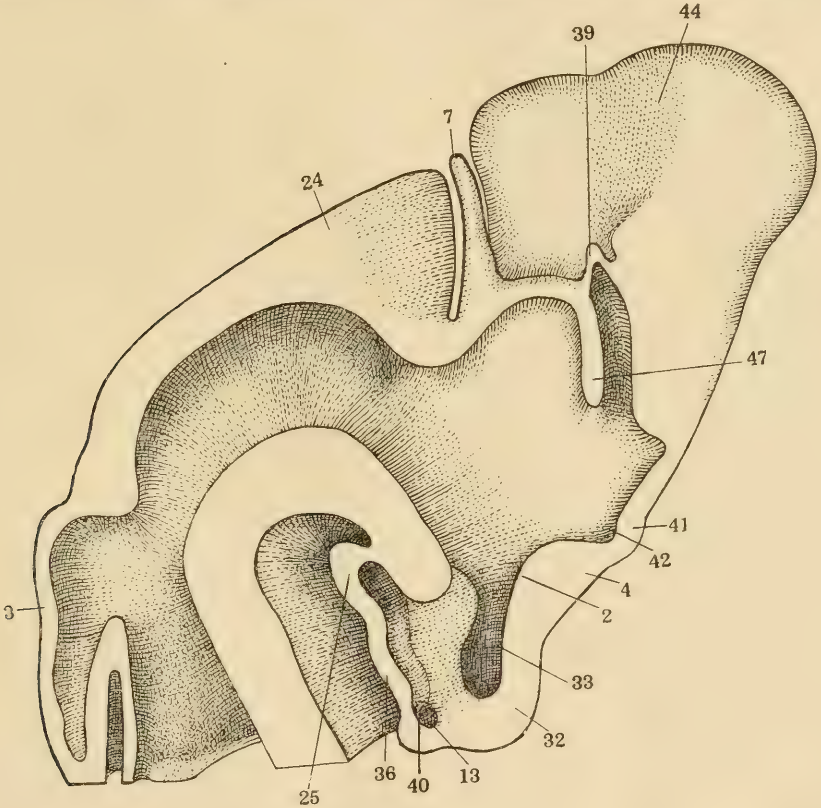

Fig. 27 Mesial view of forebrain reconstruction of 50 mm. Mustelus. × 50. The unshaded area shows the cut surfaces of the reconstruction. *2*, chiasmatic process; *4*, chiasm; *7*, epiphysis; *13*, infundibular process; *24*, mid-brain; *25*, mammillary region; *32*, post-chiasmatic eminence (lobus inferior); *33*, post-chiasmatic recess (recess of inferior lobe); *36*, post-infundibular evagination; *39*, paraphysis; *41*, supra-optic crest; *42*, supra-optic recess; *44*, telencephalon; *47*, velum transversum.

entiation of the post-chiasmatic eminence still further and makes it possible to recognize more clearly in the two lateral processes of this eminence the anlages of the *lobi inferiores*. The median post-chiasmatic groove remains as a narrow strip of the brain floor in which the tissue is relatively thin, while the inferior lobes are becoming massive, thick-walled bodies. The recess

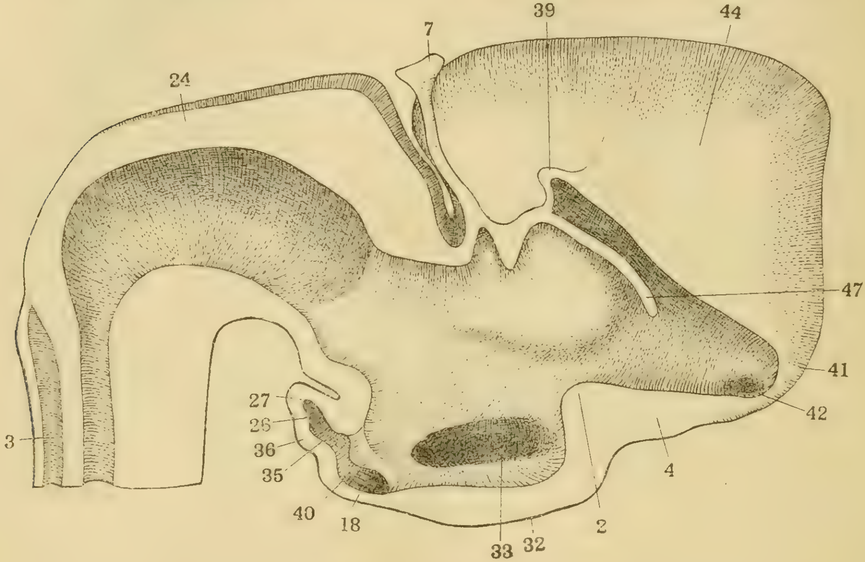

Fig. 28 Mesial view of forebrain reconstruction of 70 mm. Mustelus. × 50. The unshaded area shows the cut surfaces of the reconstruction. *2*, chiasmatic process; *4*, chiasm; *7*, epiphysis; *18*, infundibular evagination; *26*, mammillary recess; *27*, mammillary body (posterior lobe); *32*, post-chiasmatic eminence (inferior lobe); *33*, post-chiasmatic recess (recess of inferior lobe); *35*, post-infundibular recess; *36*, post-infundibular eminence; *39*, paraphysis; *40*, recess of infundibular process; *41*, supra-optic crest; *42*, supra-optic recess; *44*, telencephalon.

of the ventricle in relation with the region of the median groove extends laterad upon both sides into the inferior lobes. The chiasmatic process (*2*) has increased in size and consequently projects further into the ventricle, thus accentuating the boundaries of the prechiasmatic and post-chiasmatic recesses. The former recess may be traced laterad into a small canal which overlies the optic chiasm and the proximal portion of the optic

nerve, the supraoptic recess (*42*). The caudal portion of the infundibular region presents no change of moment. The two sprouts of the pituitary anlage which extend along the ventral surface of the median post-chiasmatic groove are still independent of each other except for a small area near their point of origin where they seem to have undergone fusion across the median line. The mammillary region (*25*) has extended to some degree laterally so that now there are added to the original median evagination of this region two slightly projecting lateral processes into which the cavity of the ventricle extends. In the 70 mm. Mustelus the inferior lobes are more prominent and the pituitary sprouts extending along the ventral surface of the median post-chiasmatic groove have now united throughout their entire length, thus forming a tongue-like projection of the pituitary gland. The mammillary region in this stage has attained all of the characteristics of the posterior lobe (*27*), presenting a median portion and two lateral processes which project free. In the caudal area of the infundibular region the only notable change is in the apparent expansion of the ventral evagination in that portion immediately ventral to the dorsal evagination. This is an area which is not in contact at any point with the pituitary gland.

Mustelus of 100 and 300 mm.; Specimens Nos. 726 and 694 (figs. 29 and 30). In both of these late stages the angle in the neural axis at the posterior isthmian sulcus has disappeared. The optic chiasm (*4*) and chiasmatic process are larger, thus accentuating the prechiasmatic (*38*), and the post-chiasmatic (*33*) recesses. The supraoptic recess (*42*) extends as a small canal along the cephalic surface of the chiasm and the proximal portion of the optic nerve. In the post-chiasmatic eminence (*32*) the inferior lobes and the median post-chiasmatic groove may be definitely recognized. In the groove rests the tongue-like extension of the pituitary gland. The posterior lobe (*27*) has increased in size, especially in its lateral processes, each of which contains an accessory recess of the ventricle. More prominent changes, however, have appeared in the caudal portion of the infundibular region and particularly in the ventral

evagination (*18*). Here growth has been more pronounced than in any other of the neighboring parts. This growth has affected the area immediately ventrad to the dorsal infundibular evagination which in this stage of 70 mm. had already shown signs of expansion. The result of the growth is the formation of an infundibular process (*13*) which consists of a smooth, membranous, but as yet non-vascular, dorsal surface not in contact with

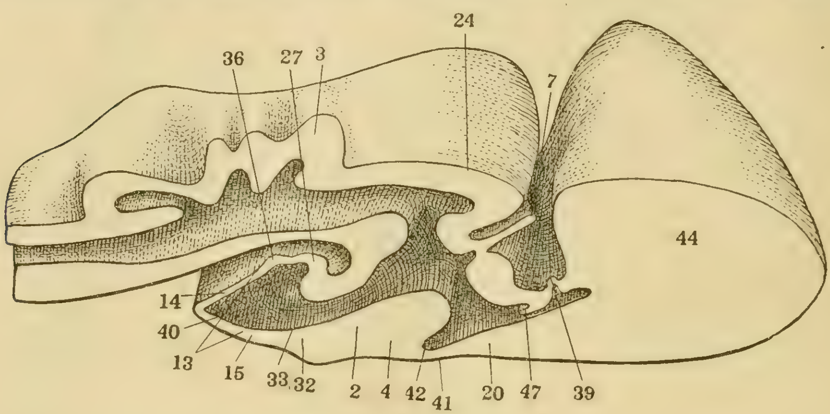

Fig. 29 Mesial view of brain reconstruction of 100 mm. Mustelus. × 25. The unshaded area shows the cut surfaces of the reconstruction. *2*, chiasmatic process; *3*, cerebellum; *4*, chiasm; *7*, epiphysis; *13*, infundibular process; *14*, infundibular process, saccular surface; *15*, infundibular process, pituitary surface; *24*, mid-brain; *27*, mammillary body (posterior lobe); *32*, post-chiasmatic eminence (lobus inferior); *33*, post-chiasmatic recess (recess of inferior lobe); *36*, post-infundibular evagination; *40*, recess of infundibular process; *41*, supra-optic crest; *42*, supra-optic recess; *44*, telencephalon; *47*, velum transversum.

the pituitary gland, the saccular surface (*14*) and a thicker surface in contact with the gland, the pituitary surface (*15*). In the 100 mm. Mustelus the saccular surface presents no sign of convolution or blood vessels; in the 300 mm. Mustelus the tendency toward the production of complicated diverticula in this surface is evident, as well as a rapidly advancing vascularization. These changes mark the inception not only of the diverticula sacci vasculosi, but also of the rich blood supply which gives the saccus vasculosus its name. In addition to the diverticula sacci vasculosi there is a portion of the recess of the infundibular

process which, because of its close relation to the pituitary gland, is called the recessus hypophyseus (*10*). The pituitary and saccular surfaces of the infundibular process are continued laterad for a considerable distance forming two tapering extensions, the lateral processes of the processus infundibuli. During this development the dorsal infundibular evagination (*36*) manifests but little change; when, however, the infundibular process is formed the dorsal evagination, because of its position, becomes the post-infundibular eminence.

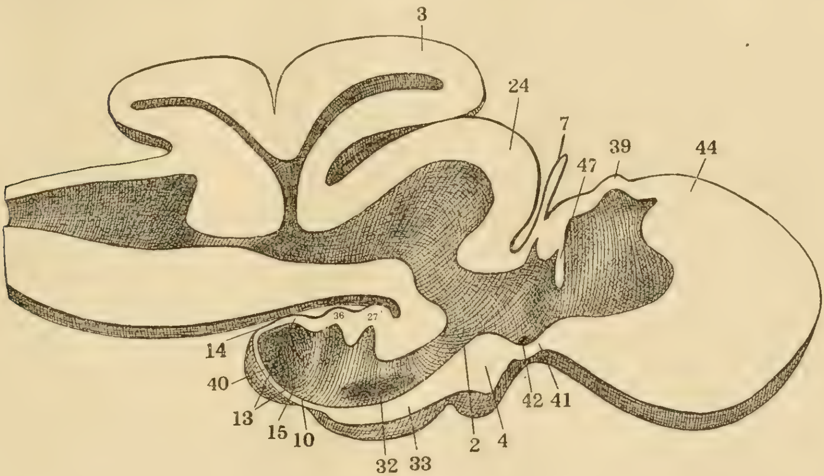

Fig. 30 Mesial view of brain reconstruction of 300 mm. Mustelus. × 25. The unshaded area shows the cut surfaces of the reconstruction. *2*, chiasmatic process; *3*, cerebellum; *4*, chiasm; *7*, epiphysis; *10*, hypophyseal recess; *13*, infundibular process; *14*, infundibular process, saccular surface; *15*, infundibular process, pituitary surface; *24*, mid-brain; *27*, mammillary body (posterior lobe); *32*, post-chiasmatic eminence (inferior lobe); *33*, post-chiasmatic recess (recess of inferior lobe); *36*, post-infundibular evagination; *39*, paraphysis; *40*, recess of the infundibular process; *41*, supra-optic crest; *42*, supra-optic recess; *44*, telencephalon; *47*, velum transversum.

The ontogenesis of the diencephalic floor in Mustelus, as in the cat and chick, may thus be traced from two primitive fore-brain elements, the optic vesicle and the mammillary region. From the optic vesicle is derived the ventral segment of the ectoptic zone which gives rise to the infundibular region. From the optic vesicle the following structures are derived, i.e., the retina,

optic nerve and chiasm, chiasmatic process, prechiasmatic and supraoptic recesses of the third ventricle. The derivatives of the ventral evagination of the infundibular region in Mustelus are the inferior lobes, median post-chiasmatic groove and the infundibular process (including the pituitary surface, the saccus vasculosus and the lateral processes of the saccus). From the dorsal evagination arises the post-infundibular eminence. The mammillary region becomes the posterior lobe.

DISCUSSION

A review of the literature covering the diencephalon reveals certain difficulties imposed upon this region by terminology. These difficulties are especially pronounced in the basal region of the interbrain, which His (10) has called the *hypothalamus*. The advantage of this term in the adult human brain, as well as in other mammalian forms, is obvious; but it loses its precision when applied to many of the lower vertebrates. There is much to recommend the term *hypencephalon* (Unterhirn) suggested by von Kuppfer (7). This, however, refers to a somewhat arbitrary subdivision of the diencephalon, and von Kuppfer himself is not always consistent in its application, since in some instances he uses it as the equivalent of the hypothalamus, while in others he restricts it to the basal area of the interbrain, exclusive of the infundibulum. The latter element, 'infundibulum,' more perhaps than any other part in this region, has been a source of confusion. Johnston's (11) objections to the use of the term 'infundibulum' seem well founded. As he points out, the application of this term to a relatively extensive embryological area and also to a much more restricted portion of the adult brain is almost certain to be misleading. Usage, however, has given it a permanency in the literature and in addition to this the phylogenetic significance attached to the part by some investigators cannot be overlooked. As already stated, Ayers (2) asserts that the hypophysis arose as an organ of taste and the infundibulum was its nerve. Boeke (19) has found in Muraenoids from the third day of embryonic life until the critical

period a sharply defined area in the ventral infundibular wall clearly differentiated to form not a gland as some maintain but a sense organ of unknown significance which is functional in the early larval stages. Other pelagic teleosts present a similar structure, although not as clearly marked as in the Muraenoids.

The ectoptic zone. It has seemed to the writer that some of the discrepancies above mentioned may arise from the fact that the 'infundibulum' in the embryological sense is not one of the primitive areas of the diencephalon. It is, as already shown in the domestic cat by Schulte and Tilney (12), a secondary derivative of the primitive optic vesicle; interpreted in this light its significance seems to become more clear. In the domestic cat, the chick and the dog-fish two primitive areas may be recognized in the developing forebrain. For a considerable period before the neural folds meet in the region of the prosencephalon the optic vesicles are the only elements present. They appear at the cephalic extremity of the neural folds as prominent diverticula, one upon either side. Almost immediately after the formation of the vesicles and before the neural folds have met, there appears a recess in the floor of the prosencephalon directly caudal of the apex of the optic evagination. This recess presents a corresponding ectal protuberance which forms the mammillary region. The optic vesicle and mammillary region are consequently the primitive derivatives of the cephalic extremity of the neural tube. These observations are true of the cat, chick and dog-fish. In the subsequent evolution of the prosencephalon the optic vesicles play the more important rôle of these two primitive derivatives. For a period prior to and for some time after closure of the neuropore this vesicle undergoes a profound remodelling, as a result of which the optic evaginations become reduced in size and an ectoptic zone appears in the form of an arc about the vesicle. This arc presents a dorsal, a cephalic and a ventral segment, the latter being the last to make its appearance. When, however, it has appeared it constitutes a well defined area, the infundibular region.

It has already been shown (p. 233) that the telencephalon arises from the cephalic segment of the ectoptic zone, while the

thalamencephalon takes origin in the dorsal segment. From these facts it seems fair to assume that the third element of this zone, namely the ventral segment, possesses similar possibilities of development and the three segments of the ectoptic zone may therefore be regarded as dynamically coördinate. The attempt to substantiate this assumption is given in discussing the derivatives of the infundibular region.

The optic vesicles. In the period of development shortly after the closure of the neuropore the floor of the forebrain consists of the lamina terminalis, the optic evaginations and the infundibular and mammillary regions. In sauropsid and mammalian forms the lamina terminalis assumes a vertical position in the later stages of development; in the ichthyopsid, on the contrary, it remains horizontal and is thus an element in the floor of the ventricle cephalad to the optic chiasm. Entally the evaginations of the primitive optic vesicles are indicated by the optic sulcus which does not in any way correspond to the preoptic and postoptic grooves of authors. This sulcus is bilateral. It does not cross the median line as the above mentioned grooves are shown to do, and in its early appearance it presents itself as an arcuate fissure consisting of a vertical and horizontal segment, the latter extending caudad to the tubercle of the floor, while the convexity of the entire arc is directed cephalad. Subsequently, when the primitive optic vesicle has become reduced by the remodelling which results in the formation of the ectoptic zone, the vertical segment of the optic sulcus disappears but the position of its horizontal segment is occupied by the optico-infundibular groove. At this stage the optic vesicle has so changed its external conformation as to have the appearance of a pedunculated diverticulum of the forebrain to which latter it is attached by a constricted, hollow stalk, the optic peduncle. In relatively late stages after the appearance of the chiasmatic process a transverse groove connects the orifices of the optic peduncles. A groove is also formed caudad to the chiasmatic process. These undoubtedly correspond to the post-optic and preoptic grooves already mentioned, but it will be noticed that their appearance developmentally is relatively late. The proximal portion of the optic

peduncle ultimately becomes expanded and contains a large recess accessory to the third ventricle which overlies the optic chiasm and proximal portion of the optic nerve. The remainder of the optic diverticulum rapidly assumes the characteristic form of the eye-cup, while the cavity between its ental and ectal layers communicates with the third ventricle by means of the optic peduncle, retaining this communication until a late period of embryonic life. Ultimately the lumen of the distal portion of the peduncle becomes obliterated. In the adults of all the forms examined a marked prechiasmatic recess of the ventricle is present. It is continued laterad along the dorso-cephalic margin of the chiasm and for some distance above the optic nerve as the supraoptic recess. The position of these recesses is indicated upon the surface by a ridge which traverses the chiasm and proximal portion of the nerve, the supraoptic crest. This likewise is constant in all the forms examined. Osborn (13), Herrick (14) and Kingsbury (15) have shown that the rudimentary condition of the eye in Necturus is accompanied by a similar condition of the optic nerve which retains the primitive lumen of the optic vesicle and is hollow for a considerable distance peripherad. This fact and the embryological evidence make clear the homologies of the supraoptic crest, chiasmatic process, prechiasmatic and supraoptic recesses in the adult.

The infundibular region. The infundibular region presents greater difficulties for analysis. These doubtless are due to the fact that the ventral segment of the ectoptic zone, like the cephalic and dorsal segments, is capable of marked adaptive variations. As seen in the elasmobranch, for example, the main feature of this region is the so-called *hypoarium* described and first so named by Sanders (16). The hypoarium consists of two large symmetrical eminences situated one on either side of the mid-sagittal line immediately caudad to the optic chiasm and containing an extension of the third ventricle. In their general conformation they are not unlike the optic lobes of the mid-brain; they are usually termed the *lobi inferiores*. In many teleosts these lobes are still further subdivided forming on either side a large lateral lobe and a small inferior lobe, both of which

contain extensions of the third ventricle. In amphibia the inferior lobes are prominent elements derived from the infundibular region, while in sauropsids and mammals the tendency to the formation of the extensive hypoarium appears to have ceased and no corresponding structures are to be found in the position of the inferior lobes. Fritsch (17) suggested the homology of these structures with the corpora mammillaria, but Herrick (14) and others have shown conclusively that this suggestion is not well founded. The significance of the inferior lobes becomes more apparent in the light of their embryological history. As already stated, the infundibular region in embryos of the dogfish, chick and cat is a secondary derivative from the primitive optic vesicles. After this region has made its appearance the portion immediately caudad to the optic chiasm undergoes certain changes which in the selachian terminate in the formation of the inferior lobes. The development of these structures as definitive elements in the floor of the diencephalon begins at a relatively late period and is characterized by the growth of a diverticulum immediately behind the chiasm in such a way that two symmetrical evaginations are formed, each containing an extension of the third ventricle. These bilateral evaginations at first have thin walls but they grow rapidly, the walls becoming thicker and the cavity contained within them being correspondingly reduced in size. In the bird the same tendency to the formation of a large diverticulum immediately caudad to the chiasm is observed. This diverticulum in the relatively late stages tends to become divided into two symmetrical evaginations and at this stage resembles in all details the early formation of the inferior lobes in the selachian. Thereafter, however, the impetus toward the formation of the typical ichthyopsid hypoarium appears to cease. The evaginations remain comparatively thin-walled and finally become a fairly prominent post-chiasmatic eminence. A similar course of events is observed in the mammal as illustrated by the development of the domestic cat. Here the infundibular region caudad to the chiasm at first forms a diverticulum which later becomes subdivided sagittally in such a way as to present two bilateral evaginations. The conditions

observed in this region in the cat embryo of 25 mm. length almost exactly duplicate those in the brain of the 20 mm. Mustelus, but as in the case of the chick, the tendency of this region to give rise to large inferior lobes diminishes as growth progresses and in the fetal stages the only evidence of this tendency is to be found in the large post-chiasmatic eminence and the post-chiasmatic recess. Significant in this connection also is the relation which the pituitary gland bears to this part of the infundibular region. As the writer (8) has already shown, the post-chiasmatic eminence in the cat and chick comes to be invested by a secondary outgrowth from Rathke's pocket which ultimately forms the pars tuberalis of the gland. In the selachian no such investment of the inferior lobes takes place, but the tuberal portion of the gland by a process of development similar to that in the bird and mammal grows forward and occupies a juxta-neural position in contact with the small portion of the infundibular region which forms the median post-chiasmatic groove.

The caudal portion of the infundibular region including the apex is involved in the formation of the neural portion of the hypophysis. In its inception the developmental process of this part in all the forms studied presents a marked similarity. The area about the apex of the infundibular region undergoes a subdivision so that two evaginations are formed, one dorsal and the other ventral. In the cat this subdivision gives the dorsal evagination the greater size from its beginning, while in the bird and the dog-fish the ventral evagination is the larger. In all instances the ventral evagination proceeds to the formation of the neural portion of the hypophysis, the infundibular process. In the salachian this process is but little pedunculated. A slight constriction does, however, occur and justifies the term infundibular process for the structure which is connected with the floor of the interbrain by a short infundibular stem. The characteristic features of this infundibular process are the development of two morphologically different surfaces one which is ventral, thin and non-convoluted coming in contact with the pituitary gland, the other which is thin-walled and dorsal in position, but

having no contact with this gland. The ventral surface because of its relations may be called the pituitary surface, the dorsal one because of its participation in the formation of the saccus vasculosus, the saccular surface. These two surfaces are present in the bird; but in the cat, although the dorsal surface of the infundibular process is much thinner than its ventral surface, there is no other evidence of the tendency toward saccus formation. As development proceeds in the selachian, the pituitary surface maintains its primitive relations unchanged while the saccular surface becomes more extensive and in Mustelus at the period of 20 cm. shows the first evidence of a rich vascularization and the tendency of its thin wall to be thrown into numerous convolutions typical of the saccus vasculosus. The pituitary and saccular surfaces extend laterad for a considerable distance, their size being reduced as they extend farther away from the median line so that they ultimately form two long tapering outgrowths, one at either extremity of the infundibular process, called the lateral processes. Similar outgrowths are observed in the development of the bird, and while no definitely corresponding structure is found in the cat, the lateral extremities of the infundibular process are much extended in a manner which seems to be reminiscent of the lateral processes in the bird and selachian. In the bird, as already shown, the dorsal surface of the infundibular process is convoluted but non-vascular; its walls are thick. All of the morphological evidence concerning it tends to show that this surface is the strict homologue of the saccular surface in the selachian, and that, whereas in the fish it proceeds to form the saccus vasculosus, the saccus formation in the bird is aborted, although the sauropsid still retains evidence of the tendency toward the formation of this structure. Furthermore, the late stages of embryonic life in the bird correspond in many details to the saccus formation as it appears in this region of the selachian.

In the mammal, as illustrated by the cat and other Felidae, there is nothing which suggests the saccus formation in any part of the infundibular process further than the very thin dorsal surface which is emphasized, in the early stages, by the rapid

growth and thickness in the ventral wall of the infundibular process. This, together with the fact that in the Felidae an extension of the third ventricle is contained in the infundibular process, points strongly to the conclusion that the dorsal wall of this process in embryonic stages may be homologized with the saccular surface just described in the other forms. That this area in mammals becomes invested by the pars infundibularis of the pituitary gland, may be interpreted as causing the retrogression of the saccular surface and its replacement by a new area in contact with tissue of the pituitary gland, due to the greater extension of the infundibular portion of this gland in mammals.

Discussing the significance of the saccus vasculosus and its more characteristic formation in the water-living types of reptiles, Edinger (18) suggests that it may be an apparatus of especial importance to aquatic animals. This inference, however interesting, is not borne out by the facts observed in some of the aquatic mammals, since there is no evidence of anything corresponding to the saccus vasculosus or even an abortive saccus-formation in Castor canadensis or in Macrorhinus angustirostris. The absence, therefore, of any attempt to revert to the formation of a saccus vasculosus in mammals, even though they be water-living, fails to corroborate Edinger's suggestion that this apparatus is an adaptation peculiar to aquatic life. It seems more probable that the disappearance of the saccus vasculosus depends upon a profound remodelling of the forebrain which occurs in passing from ichthyopsid to the sauropsid and mammalian forms. It is not unlikely that this highly vascularized structure is closely related to if not identical with the chorioid formations and represents in the fish a means of supplying an extensive chorioidal plexus to the third ventricle, particularly as such plexuses are relatively small in other parts of the diencephalon.

The dorsal evagination of the infundibular region still remains to be considered. As already stated, this evagination in the cat is of greater size than the ventral one from which latter the infundibular process is derived. In the bird and the dog-fish

the reverse is true. The evagination is present in the early stages in the selachian and may be traced through to adult life, when it occupies a position immediately ventral of the posterior lobe and dorsal to the saccus vasculosus. Similarly in the bird it lies dorsal to the infundibular process from its inception and maintains this position in the adult. Its development in the cat is equally clear; here it forms a protuberance of the diencephalic floor caudal to the infundibular stem and in front of the mammillary bodies; this has been called by the writer the post-infundibular eminence. Much discussion has arisen concerning this element of the interbrain. Retzius (9), who first described it in mammals, considered that it was the homologue of the saccus vasculosus in fishes. Staderini (20), however, states that topographically, as well as from its developmental relations, the saccus vasculosus can bear no relation to the *eminentia saccularis*. It is also his opinion that nothing in the intimate constitution of the saccular eminence favors the conception of Retzius. In fishes the saccus vasculosus is a thin-walled structure connected with a great number of blood vessels. In man and other mammals the structure referred to by Retzius is a relatively thick-walled evagination with scanty vascularization. Sterzi (21) is unwilling to accept the interpretation of Retzius given to the eminentia saccularis, and believes that the saccus vasculosus has nothing in common with the latter either in position or structure, while Perna (22) on histological grounds maintains that there can be no homology between the saccus vasculosus and the so-called 'saccular eminence.'

The post-infundibular eminence has been shown in illustration by many authors in a number of different species, although it has not always been definitely referred to in their text. Herrick and Obenchain (23) in their reconstruction of the brain of Ichthyomyzon concolor figure a small, unleadered eminence ventrad to the mammillary body, in which there appears on mid-sagittal section a small recess communicating with the third ventricle. The only reference to this element made by these authors is the attention which they call to the fact that the *post-infundibular commissure* passes through the more cephalic portion of the structure.

In surface relief, however, it forms a prominent element in their illustration of the diencephalic floor in this form. Sterzi (21) in his illustrations of Acanthias vulgaris (80 cm. long), in Mustelus laevis (30 cm. long) and in Raja clavata (60 cm. long) shows a similar structure dorsal to the saccus vasculosus and ventral to the posterior lobe although in none of these cases has he included this element in his description. Burckhardt (24) shows a similar condition in Protopterus annectans. In the ontogenesis of the dog-fish, of the chick and of the cat the dorsal evagination of the infundibular region is a constant element and may be traced through successive stages until the definitive post-infundibular eminence has made its appearance. Thus the embryological history of the infundibular region seems to make clear the fact that the inferior lobes may be homologized with the post-chiasmatic eminence. The infundibular process, including as it does the saccus vasculosus of the ichthyopsid, is the homologue of the infundibular process in the sauropsid and mammal, although in these latter forms the saccus formation is retrogressive or absent. In this respect the writer agrees with Johnston (11) and concurring with him can find no evidence to support Edinger's (18) idea as embodied in his schematic figure of a sagittal section of the vertebrate brain which shows an infundibular process in contact with the pituitary gland while dorsal to it is an entirely separate evagination of the brain floor which he calls the saccus vasculosus. It seems equally clear that the homology of the post-infundibular eminence may be established throughout the phylum. That it is an element separate and distinct from the saccus vasculosus is evident from the ontogeny of the selachian in which both a saccus vasculosus and a post-infundibular eminence are present. There can be no grounds, therefore, for the homology suggested by Retzius (9) between the 'saccular eminence' of mammals and the saccus vasculosus of fishes.

Although the fact has not been fully established, the evidence furnished by the ontogenesis of the dog-fish, of the chick and of the cat strongly suggests that the derivatives of the three segments of the ectoptic zone are coördinate. In this light the

telencephalon derived from the cephalic segment, the thalamencephalon from the dorsal segment and the infundibular region from the ventral segment are developmental equivalents. It has been shown that from the infundibular region in the ichthyopsid the inferior lobes, the infundibular process and the post-infundibular eminence are derived. If, as has been assumed to be the case in fishes, the inferior lobes are chiefly concerned in the gustatory sense, the telencephalon in the olfactory sense and the thalamencephalon in the somaesthetic senses, then there is further reason to believe that the derivatives of the three segments of the ectoptic zone are functionally of the same order. The disappearance of the inferior lobes in passing from the ichthyopsid to the sauropsid is, as a process, no more difficult to comprehend than the similar disappearance of the optic lobes of the midbrain in the transition from the bird to the mammal. In each instance this process seems to be accomplished by the addition of neopallial areas which assume the functions of the more primitive brain parts. The significance of the persistence of the infundibular process and the post-infundibular eminence is less clear, although in the former case this doubtless is involved in the adaptive variations of the pituitary gland, while in the latter the post-infundibular commissure may be a determinative factor.

The tuber cinereum is usually described as an area in the basal region of the diencephalon, bounded cephalad by the optic chiasm, caudad by the mammillary bodies and laterad by the optic tracts and cerebral peduncles. This area in mammals includes the post-chiasmatic eminence, the lateral eminences and the post-infundibular eminence. From the embryological standpoint, the tuber cinereum comprises all of the derivatives of the infundibular region except the infundibular process and its stem. To hold the tuber to this interpretation in fishes and amphibia would necessitate the inclusion in it of the inferior lobes, but since this has no apparent advantage in the lower forms mentioned it is, perhaps, well to confine the term *tuber cinereum* to mammals, in which instances it is useful in referring to a distinctive region of the diencephalic floor. The homology of the

lateral eminences of the tuber is not clear in the light of the material studied. Conditions in the teleost, however, in which the hypoarium presents small lobi inferiores and much larger lobi laterales, may be regarded as suggestive, since the progressive reduction of the inferior lobes has been shown to result in the formation of the post-chiasmatic eminence and a similar diminution of the lateral lobes might, therefore, determine the eminentiae laterales hypencephali. This homology is tentatively offered, since it requires further proof in the development of the teleost to establish it.

The mammillary region. The posterior lobe is the most caudal structure in the diencephalic floor of the selachian. Its relations have already been described (page 231). It consists of a median portion and two lateral processes which project free, one upon either side. Its characteristic feature appears in the fact that it contains a large recess of the third ventricle which extends from the median portion into the two lateral processes. Sterzi (21) has figured and described the posterior lobe in selachians; von Kuppfer (7) has shown it in Bellostoma, Squalus acanthius, and Necturus. Edinger (18) describes it in the selachian as the lobus posterior sive saccus infundibuli. Johnston (11) shows the posterior lobe as well as the post-infundibular eminence in a figure of the mesial surface of the right half of the brain in Squalus acanthius, although neither of these structures is specifically named by him in this place. Herrick and Obenchain (23), in their illustration taken from the reconstruction of the brain in Ichthyomyzon concolor, indicate a structure similar in relations and characteristics to the posterior lobe which they call the corpus mammillare. In several respects the designation given the structure by the last named authors seems to be most in keeping with the facts, for although the majority of investigators have employed the term *posterior lobe* in selachian and teleosts, the embryological history of the structure clearly shows that it is derived from the primitive mammillary region. In the ichthyopsid the mammillary region develops in such a way as to form a posterior lobe presenting the characteristics already described and retaining a recess accessory to the third ventricle,

the recessus lobi posterioris. In birds and reptiles the developmental history of the mammillary region through the early stages is similar to that in the fish. Later, however, the walls of this region begin to thicken rapidly and the mammillary recess becomes progressively reduced in size until it is obliterated and the solid mammillary bodies have been formed. The marked cephalic flexure in the fowl causes a divergence in the long axes of the mammillary bodies caudo-cephalad, so that these structures do not present the same prominence here as they do in the diencephalic floor of mammals. The development of the mammillary region in the cat manifests certain peculiarities which I was unable to observe in either the chick or the dog-fish. These peculiarities appear in the formation of two relatively early diverticula, the median mammillary evagination and the dorsal mammillary evagination. The latter evagination is unquestionably involved in the formation of the *corpus interpedunculare*, for I have found that the fasciculus retroflexus of Meynert may be seen passing from the *habenular region* directly to the evagination in question as early as the stage of 25 mm. There can be no doubt that this dorsal evagination, therefore, is the anlage of the corpus interpedunculare. That no similar evagination has been found either in the dog-fish or in the chick may argue that a less definite portion of the mammillary region gives rise to the corpus interpedunculare in these forms, but it is probable that this ganglionic body takes origin from the primitive mammillary region, even though no distinct evagination of its own is formed. To establish this supposition, however, it will be necessary to study the development of this region further, particularly with a view to the ontogenesis of the fiber tracts connecting the several centers involved. In the light of these facts, with the exception of this interpeduncular element, it seems warranted to homologize the ichthyopsid posterior lobe with the mammillary bodies of sauropsids and mammals.

CONCLUSIONS

The supraoptic crest, chiasmatic process, prechiasmatic and supraoptic recesses in the mammal have their definite homologues in the sauropsid and ichthyopsid.

Of the structures derived from the ventral segment of the ectoptic zone the post-chiasmatic eminence of the mammal and bird may be homologized with the inferior lobes or hypoarium of fishes, while there is some evidence which seems to indicate that the eminentiae laterales hypencephali are the homologues of the lateral lobes of teleosts.

The derivatives of the caudal portion of the infundibular region, including its apex, are the infundibular process and post-infundibular eminence.

The infundibular process in the selachian presents a pituitary and a saccular surface, the latter forming the saccus vasculosus. In the bird these two surfaces are present; the saccular surface, although it has some of the characteristics of a saccus-formation, does not present an actual saccus vasculosus. So far as may now be stated for the condition in mammals, the Felidae present an extensive pituitary surface in their infundibular process. The saccular surface, however, has lost all characteristics of saccus-formation and is in fact invested by tissue of the pituitary gland. In other mammals it is difficult to draw distinction between the pituitary and saccular surfaces of the infundibular process, and this differentiation in Mammalia would indeed be impossible were it not for the intermediate position of the Felidae in this respect between the bird, on the one hand, and the majority of mammals on the other. The lateral extensions of the infundibular process, the infundibular recess, infundibular stem and infundibular canal of the domestic cat all have their homologues in the bird and selachian. The disappearance of the saccus vasculosus from the mammal may be traced through several stages of retrogression from the dog-fish to the cat, so that the homology of the infundibular process as a whole in the mammal with that of the selachian seems to be warrantable.

The post-infundibular eminence of the mammal seems to bear a clear homology to that of the bird and selachian. The embryological evidence concerning the development of this region is strongly suggestive if not conclusive in establishing this homology. The same facts make it impossible to consider the post-infundibular eminence as phylogenetically related to the saccus vasculosus, and hence raise serious objection to the term 'eminentia saccularis' as applied to it.

There can be little doubt that the posterior lobe of the selachian is the homologue of the mammillary body in the bird and mammal.

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A TRACTUS OLFACTO-TEGMENTALIS IN THE HUMAN FETAL BRAIN[1]

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NINE FIGURES

It is commonly taught that the most direct pathways over which impulses aroused in the olfactory centers may reach the motor centers are the two following:

a. From the olfactory centers in the forebrain to the tuber cinereum or the corpus mammillare, and from these to the tegmentum or possibly to motor centers directly;

b. From the forebrain centers to the nucleus habenulae, thence over the bundle of Meynert to the interpeduncular nucleus and thence to motor centers over paths not well known.

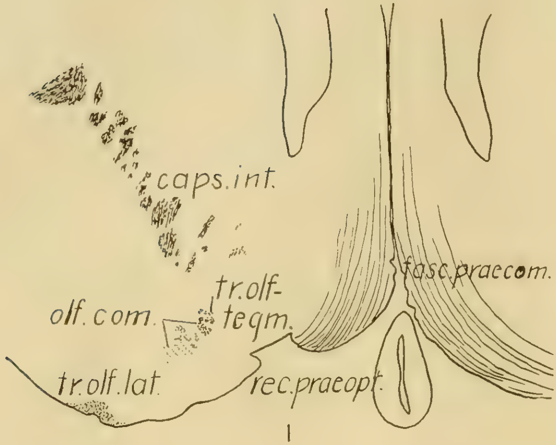
The following description adds to the evidence that a connection exists between the olfactory and lower centers without interruption in the diencephalon.

The brain studied is that of a fetus 145 mm. in length, crown-rump measurement. It was received fresh and fixed in 15 per cent formalin. Sections were cut transverse to the long axis of the hemispheres and lengthwise of the brain stem, 50 microns in thickness, and stained with Delafield's hematoxylin. The preservation proved to be excellent.

The brain at this age is largely composed of cell-masses which are deeply stained. The fibers take little stain and where definite bundles are present, these stand out sharply among the cell-masses and neuropile. Certain well known tracts, such as the bundles entering into the anterior commissure and the fornix, are very clearly defined in this brain.

In a section passing just rostral to the anterior commissure (fig. 4) we see on the right side the precommissural fibers of the

[1] Neurological Studies, University of Minnesota, No. 20, April 1, 1915.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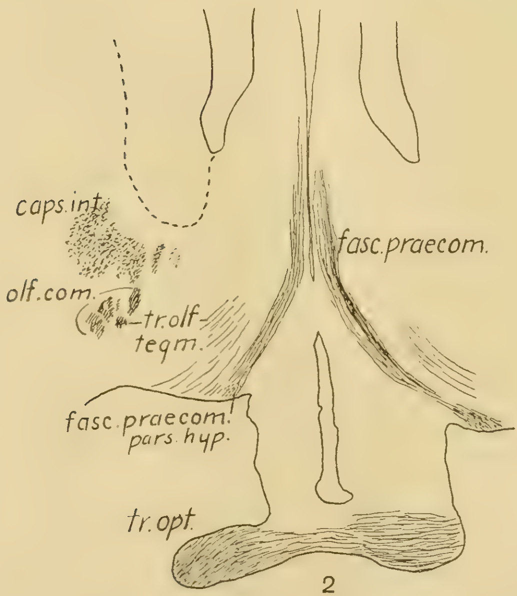
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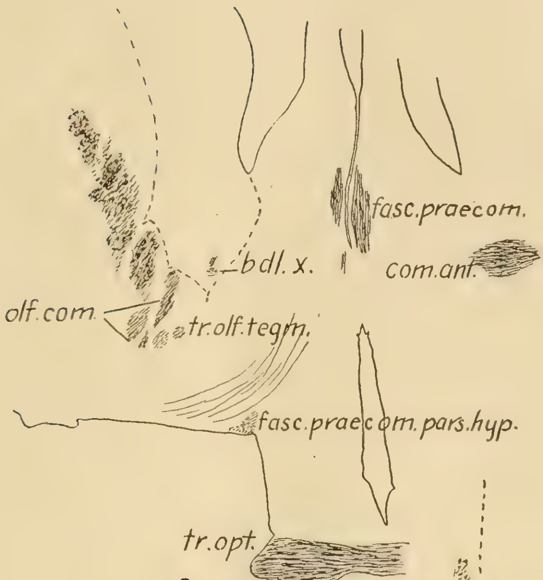
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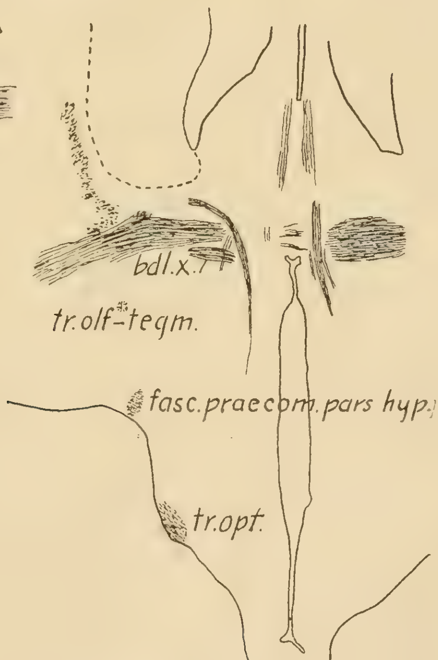
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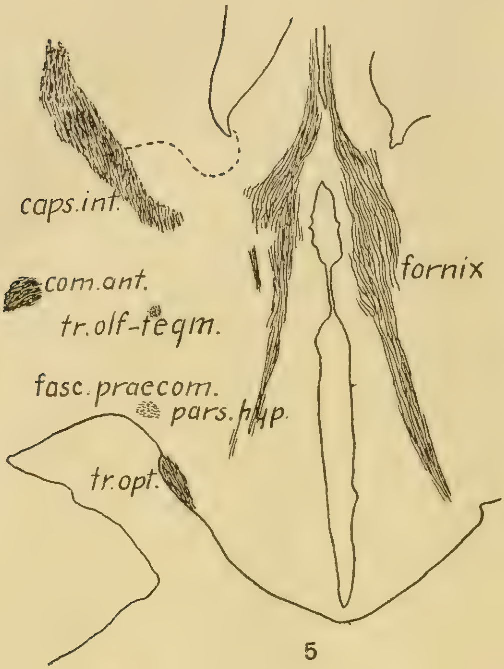
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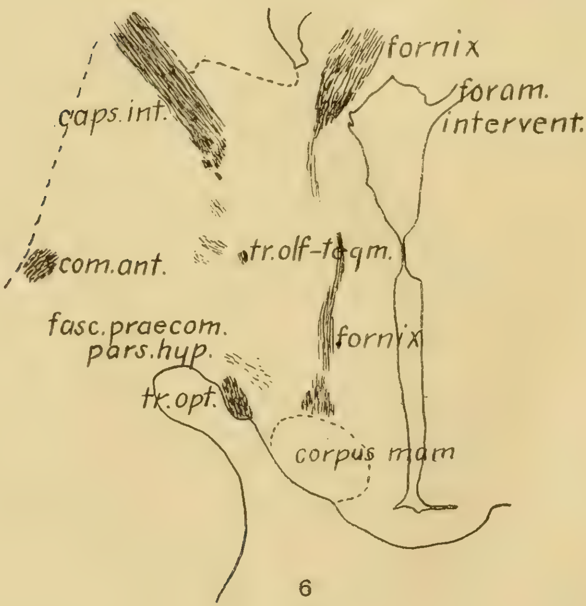
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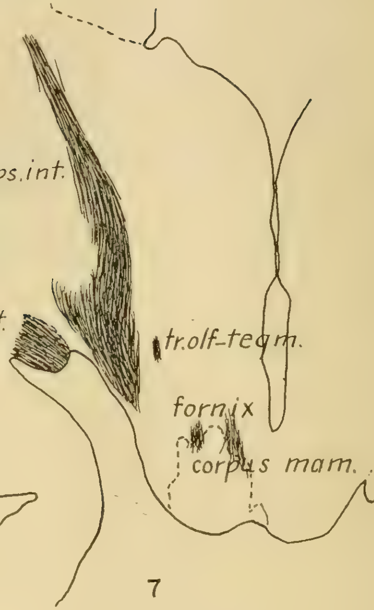
fornix crossing the anterior commissure vertically. On the left side appear a larger and a smaller commissural bundle. The smaller (*bdl. x*) is one of the olfactory bundles of the anterior commissure which crosses the mid-line independently of the main body of the commissure. Crossing these two bundles in a sweeping curve is a small bundle which runs down into the tuber cinereum. When this small bundle is traced rostrad it joins the smaller commissural bundle (fig. 3). Hence, a small bundle separates from the olfactory commissure, passes over the anterior commissure and enters the tuber cinereum. This condition has not before been described so far as the writer is aware.

In the section described there appears beneath the limb of the anterior commissure a fair sized bundle almost round in transverse section (*tr.olf-tegm.*). When this bundle is traced rostrad it is found that it intermingles with the olfactory bundles of the anterior commissure and has a commmon origin with these. This is illustrated in figures 1, 2, and 3. While some fibers may enter these bundles from the olfactory tract, there can be no doubt that most of the fibers are directly related to the olfactory tubercle and adjacent secondary olfactory centers.

The course of this bundle caudal to the level of the anterior commissure is shown in figures 5, 6, 7, 8, 9. The bundle is symmetrical on the two sides, but only the left side is drawn. It runs along the inner face of the internal capsule and descends somewhat into the hypothalamus until it comes to lie between the terminal portion of the fornix and the internal capsule (fig. 7). Beyond the mammillary body it rises again and gains a position dorsal to the medial border of the crus (fig. 8). The bundle then continues between the substantia nigra and the nucleus ruber and divides into several fascicles. These fascicles while continuing spinalward turn rather rapidly dorsad and somewhat laterad. They become imbedded in small masses of cells and are lost just at the upper or anterior border of the pons (fig. 9). One fascicle seems to enter the dorsal part of the pontile gray (fig. 9). One or two fascicles run much farther dorsad than the others, but do not approach so near the brachium pontis.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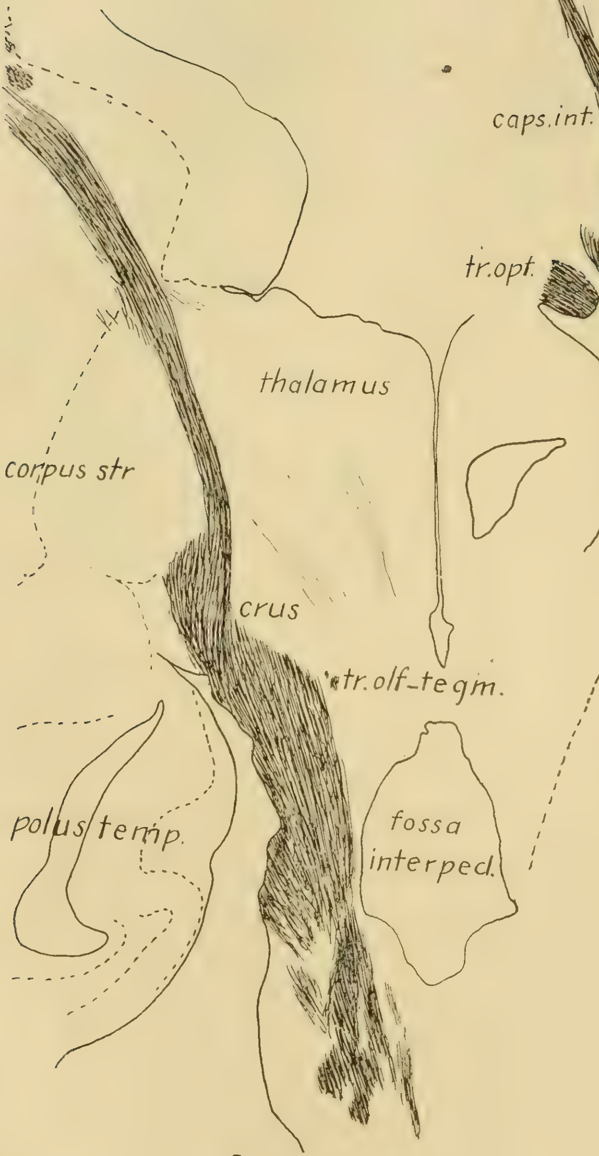
thalamus
corpus str
crus
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polus temp.
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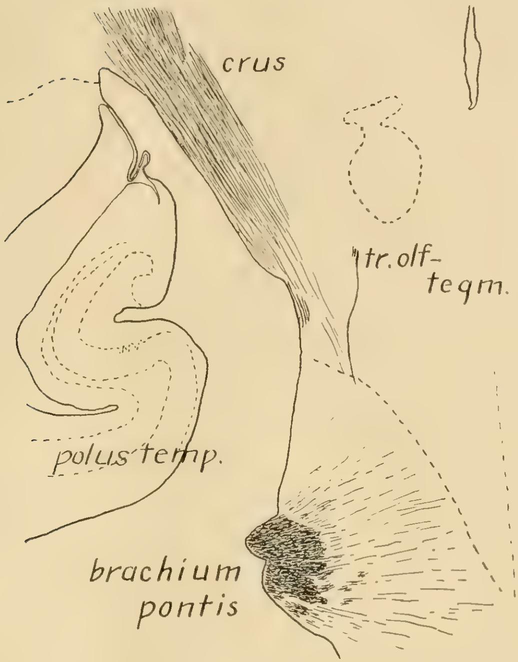

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The bundle described is interpreted as a descending tract from the olfactory centers to the motor-correlation centers in the tegmentum at the level of the isthmus. Such preparations give no direct evidence, of course, as to the actual origin and endings of the fibers. At their rostral end the fibers of this bundle are indistinguishably intermingled with the fibers of the olfactory commissure which we know arise from the olfactory centers. At its caudal end the fibers spread widely in the tegmentum. This renders it very improbable that the fibers arise in any of the sensory nuclei, such as the nucleus of the trigeminus. Its behavior rather suggests the breaking up of a bundle at its place of ending.

From the facts just stated the writer can see no reason for comparing this with the quinto-frontal bundle described by Wallenberg. That bundle is supposed by Edinger (Vorlesungen, 1908) to carry impulses from the sensory nucleus of the trigem-

inus to the tuberculum olfactorium, which serves as a correlation center for oral and nasal sensory impulses (muzzle-sense). If this were the function of the tuberculum olfactorium, one would expect that in forms like man, in which the olfactory apparatus is reduced and the oral sense is very important, the tubercle would be large relative to the other olfactory centers. Such is not the case. On the other hand the forms in which the tuberculum is large are those in which the olfactory apparatus is very large (Ornithorhynchus, Didelphys, dog).

There is more reason for comparing this with the descending bundle mentioned by Edinger (1908, pp. 123, 286) as arising in the lobus parolfactorius and running through the dorso-lateral part of the oblongata, to the cervical cord, tractus fronto-bulbaris. Edinger's lobus parolfactorius is a large, illy defined region "which includes the whole base of the brain" (p. 252), and there is nothing to indicate from what part of this area the tractus fronto-bulbaris arises. Also, it seems fairly certain that the bundle above described ends largely or wholly at the level of the isthmus. It is quite possible that some of its fibers pass on to the cervical cord and that these constitute the tractus fronto-bulbaris of Edinger.

Figures 2 to 6 show another bundle of considerable interest which is clearly defined in this series. This is the bundle of precommissural fornix fibers which enter the hypothalamus (*fasc. praecom. pars hyp.*). These constitute the most compact bundle in the system of vertical fibers in the "septum" rostral to the anterior commissure (fig. 2). The bundle is conspicuous in the sections back to the level of the optic tract, which it crosses to enter the lateral wall of the tuber cinereum. Whether the fibers reach the mammillary body can not be determined in this specimen.

CORTICAL LOCALISATION AND FURROW FORMATION

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ONE FIGURE

The study of cortical localisation, whether by the more popular microscopical methods of Brodmann, Campbell, Bolton, Mauss and others, or along the macroscopical lines laid down by Elliot Smith, has raised many points of great interest. Not the least important of these is the question of the relationship of the cerebral furrows to the various specialised areas. Anatomists are divided into two camps: Those who believe that the furrows are produced purely by growth antagonism and those who claim chief importance for the influence of local differentiation. It will be shown below that both of these factors have a marked influence, and it will be our present endeavor to examine just what value each of the two has, first in the primate brain and then in lower brains.

With regard in the first instance to cortical differentiation. It will be seen that this factor is unsatisfactory as the sole producer of furrows, for it does not always lead to furrow formation. Brodmann (4) has recently published surveys (fig. 1) of two of the lower monkeys (Hapale jacchus and Lemur niger), both of which have neopallial surfaces showing distinct histological areas. Yet neither of them has many furrows; Hapale jacchus has no sulcus centralis, for instance, although the animal possesses sharply defined motor and sensory areas, and this furrow is but dimly fore-shadowed in the Lemur named. If cortical specialisation was sufficient in itself to produce furrows, then any animal which had more than one area on its brain (and what animal has not?) should have corresponding furrows to limit the boundaries of those areas, or to be enfolded axially along them, to use Elliot Smith's terminology. As we have just seen—and many other examples could be cited—this is not the case.

Further, the maximum and minimum thickness of the gray matter of man are about 4.0 mm. and 1.25 mm. respectively. So that the maximum depth of the furrow that could run between contiguous areas, if specialisation were the only cause of furrows, would be 2.75 mm. This in itself is enough to show that other factors besides cortical specialisation are involved in the production of the sulci.

With regard next to growth antagonism: It is evident that growth antagonism must play an important part, otherwise all the areas would be spread out evenly upon the surface of

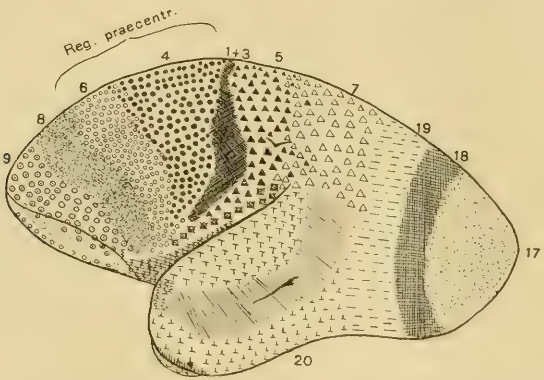

Fig. 1 Cortical map of Marmoset, Hapale jacchus [K. Brodmann (5)]. Shows that specialisation alone is not sufficient to produce furrows. When these areas have increased in extent and new ones have been added, furrows will have to appear. Their sites can already be forecasted on this map, as the edges of the areas correspond remarkably with the position of the furrows in higher brains.

the brain, and fissures would be absent. This state of affairs is almost possible in the lower monkeys whose cortical surfaces have but few areas to accommodate, and accordingly in their case the brain is to a large extent smooth. In the human brain, where place has to be found for upwards of forty distinctly different histological areas, the displaying of all these areas in toto is impossible, as an enormous cranium would be necessary. Only some 36 per cent of the cortical areas are exhibited on the surface of the human brain: 64 per cent are hidden in the furrows (4). This means that the cranium would have to be three

times the size that it is at present if man were to have a smooth brain, and would necessitate a head so much heavier that the whole skeleton would have to be remodelled to support it. The figures just given show the immense importance of growth antagonism as a causative factor in the production of the cerebral furrows. But growth antagonism between the expanding cortex and its fibro-osseous capsule is not sufficient in itself to account for the whole story of furrow formation in the primate brain, in which the furrows on the whole are remarkably constant. If the formation of sulci depended alone on the crumpling of a plastic surface to accommodate itself to a limited space, the furrows so formed would be not necessarily the same in any two brains. The constancy of position, length, inclination, and direction, of the cerebral sulci of man and the anthropoids denotes a mode of origin less fortuitous than this.

It is evident, then, that the necessity for the appearance of furrows at all arises from growth antagonism, but we must look to architectural changes in the gray matter as the guiding influence in the *placing* of the furrows. It is of course true that the edges of the areas and the sulci do not always correspond with mathematical precision. On the other hand, the remarkably close relationship between the two is one of the most striking facts that the cortical maps have brought out. Until comparatively recently the furrows were taught to students with great zeal as more important than the gyri. We now realize that the two are causally interdependent. When we have more cortical maps, so that an average can be taken and boundaries finally decided upon, it may well be that we shall be able to map out the various areas free-hand from the sulci alone. This is to a large extent possible to-day, as in the case of motor, sensory, visual and parietal areas.

GROWTH ANTAGONISM

This is a phrase which needs some explanation. Literally it means antagonism between (in this case) a rapidly expanding cortex and its limiting capsule. But we shall not be viewing it in the proper perspective unless we attempt to realize how

it has come about that there should be any antagonism at all between the brain and the skull. Antagonism, as will be seen below, is practically absent in Prosimiae, but is present to a marked degree in man owing to the many new areas he has acquired. Hence a better phrase would be 'evolutionary antagonism', particularly as there is much evidence to show that the human skull and brain are markedly in sympathy,[1] as it were, as regards growth in any individual case although the space allowed the brain is small. So that 'growth antagonism' is a misleading term in some respects. It must be remembered that there are two integral factors involved in growth antagonism: (1) Rapid cortical expansion; (2) Limited intra-cranial space. Either of these two factors is capable of profoundly influencing the amount of furrow formation and convolution. But it seems as if Nature had regulated these factors for each order. As we shall see, it seems as if the intra-cranial space was relatively set for all the primates, whilst the amount of cortical expansion is gradually increased. In other orders different arrangements are made. All histological evidence as embodied in cortical maps, supports the fact that the human brain is richer in areas than that of any other animal. Difference of histological structure and difference of function seem to be closely allied. For as we trace the brains of the animal scale upwards and new functions are seen to be acquired we find that the gray matter increases in extent, in area, and not in thickness. Brodmann has shown that in certain Prosimiae whose brains are poor in special areas the amount of cerebral surface to be accommodated and the amount of room provided are not much discrepant, so that only 7 per cent of the total surface has to be infolded in furrows. In the anthropoids so many new areas to house new functions have arisen that the discrepancy is much greater, whilst in man the quantity of brain surface in excess of the accommodation has risen to be two-thirds of the whole (see table 1). Thus man's brain is more highly convoluted than that of any of the primates, because the increased area of neopallium

[1] I refer here to cases of arrested cerebral development and coincident microcephaly, and the reverse.

lodging the newly acquired functions has not been accompanied by a proportionate increase in the intra-cranial space provided.

A study of Brodmann's interesting table (4) (see next page) in full shows a remarkably gradual and progressive diminution in convolutioning as we descend through the primates to the lowest monkeys. It is therefore probable that the factors in furrow formation are the same and are constant throughout the primates, otherwise the downward procession would not be so orderly. The probable cause of this is to be found in the fact that in the primates the cranial capacity remains relatively more or less constant, whilst the surface area to be accommodated gradually increases from the Lemurs to man, so that more and more furrows arise.

The new areas that make their appearance in the anthropoids are the association areas. In 1913 the writer (1) (2) (3) pointed out that the parietal field was a new acquisition in human and anthropoid brains and therefore that the furrows traversing this area were new formations too and could have no homologies on lower brains. Ingalls (6) has since confirmed this. The prosimian neopallium is almost entirely composed of the motor and the various sensory areas, each surrounded or contiguous with its corresponding "psychic" area (Flechsig and Bolton). Whilst in the higher brains these areas become widely separated notably by the development of the posterior association field. In spite of the appearance of this large new area behind the central sulcus the furrow is placed further back (more caudally) on the human brain than on the lower ones. Brodmann (5) has shown this to be due to the great increase in extent of the regio frontalis (proper). So that with these new areas to be accommodated it is not surprising that the human brain should be more highly convoluted than the lower, since the intracranial space has not increased coincidentally with it. It must be granted that when furrows do appear they tend to do so at the edges of the specialised areas, as Elliot Smith (7) was the first to point out. Difference of structure necessarily denotes a difference of texture, as we know in civil life from our experi-

TABLE 1

Total cortical surface, cortex in furrows, and brain weight of various mammals

ORDER, ETC.	GENUS, ETC.	TOTAL CORTICAL SURFACE OF A HEMISPHERE IN SQ. MM.	FURROW CORTEX		BRAIN WEIGHT IN GRAMS. (HEMISPHERES IN BRACKETS)
			Area in sq. mm.	Per cent of total cortex	
Man	European Maxim.	135,470	91,667	67.7	1590 (707)
	European Minim.	101,918	63,148	62.0	1327 (590)
	European Average	112,471	74,328	64.6!	- -
	Native Average	96,578	58,558	60.6	- -
	Idiots Average	66,800	37,992	56.9	-
Anthropoids	Chimpanzee (Anthropopithecus)	39,572	25,985	65.7	295 (122)
	Gibbon (Hylobates)	16,301	9,330	57.3	118 (47)
Lower monkeys (Pithecidae)	Cynocephalus	21,321	12,290	57.7	158 (63.5)
	Cercopithecus	1,649	7,526	51.4	106 (46)
	Hapale jacchus	14,641	221	14.6	7.5 (3.5)
Prosimiae	Lemur	4,054	1,583	39.1	28.3 (9.8)
	Chirogaleus	921	75	8.1	5.3 (2.1)
Carnivora	Bear (Ursus)	29,840	14,809	49.6	350 (142)
	Lion (Felis leo)	21,792	10,581	48.6	259 (85)
	Dog terrier (Canis)	9,527	3,785	39.7	63–5 (26.5)
	Cat (Felis)	4,474	1,763	39.4	31 (12)
	Weasel (Mustela)	5,066	2,364	46.7	27 (11.2)
	Pole-cat (Putorius)	2,454	950	38.7	10.7 (4.1)

TABLE 1 (continued)

ORDER, ETC	GENUS, ETS.		TOTAL CORTICAL SURFACE OF A HEMISPHERE IN SQ. MM.	FURROW CORTEX		BRAIN WEIGHT IN GRAMS (HEMISPHERES IN BRACKETS)
				Area in sq. mm.	Per cent of total cortex	
Ungulata	Elephant	(Elephas)	301,843	222,521	73.7!	4925 (1650)
	Horse	(Equus)	56,995	37,398	65.6	590 (235)
	Ox	(Bos)	49,849	30,199	60.6	540 (225)
	Sheep	(Ovis)	14,014	7,889	56.3	118 (45)
	Pig	(Sus)	13,022	6,509	49.9	112 (43)
	Goat	(Capra)	12,005	5,376	44.8	105 (40)
Cetacea	Porpoise	(Phocaena)	46,994	31,339	66.7!	455 (173)
	Seal	(Phoca)	27,551	17,768	64.5	187 (75)

ence of fabrics. So that when furrows must occur, their position, length, and direction are determined by differences of architecture in the gray matter. But the depth of the furrows, and what is synonymous with this—the amount of cortex buried in the sulci, is determined by the amount of growth antagonism present. In other words, in the primates furrows are necessarily produced because a great number of cortical areas have to be housed in a small space and the depth of the furrows will depend on the amount of discrepancy between the volume of the occupier and the space to be occupied.

It must be remembered that a furrow is not an entity in itself any more than dyspepsia is a disease. Both are symptoms—the furrow of evolutionary changes in the cortex. It will be quite evident in the light of modern knowledge that the much discussed (6) temporary furrows are post-mortem artifacts, as Hochstetter and Elliot Smith have shown.

So much for furrow formation in the primates.

A glance at the accompanying table will reveal a very curious fact, that there are brains more rich in sulci and gyri than man's, and this in animals much further removed from him than his ancestral primates. Thus certain of the carnivora, ungulates and cetacea, have brains distinguished by an extraordinary luxuriance of convolution. And it is very confounding at first to observe that the elephant, horse, and probably the whale (Brodmann) have more convolutions than man. It is impossible to concede that the brains of these animals can be so rich in areas as many of the lower apes, not to mention man, in spite of the so-called sagacity of the elephant, horse and dog. Cortical maps of these animals are not yet forthcoming,[2] since attention has been very naturally fixed first on the primates. Yet the only logical inference that can be drawn in the case of the genera now under discussion is that furrow formation in their case must depend on factors different from those just laid down for the primates. And since cortical specialisation has presumably not reached a high point in them, we must look to the

[2] Brodmann refers to surveys of the dog's brain by himself and by his colleague Scharff [(5). p. 179]. He gives no reference.

second factor in growth antagonism—restricted intracranial space—as the chief cause. The skulls of all these animals named are adapted to special purposes—that of the carnivora for the seizing and killing of prey, necessitating very powerful temporal muscles with great buttresses of bone to give wide origin to them. In the ungulates the head is modified for the cutting of food from the surface of the ground and for providing a large area for the grinding of herbs.

In the cetacea the head end of the body has to be kept small to enable the animal to plough the water with the least possible resistance, whilst at the same time these animals possess an enormous body weight which has to be represented in their brains. So that it is not surprising that the amount of convolutioning in the cetacea should be, as it is, greater than in the carnivora and most of the primates. In the primates the existence of the prehensile paw allows the skeleton of the face to be reduced to a minimum so that more space can be allowed the brain, and the weight of the skull still be within supportable limits.

CONCLUSIONS

1. That to say that furrow formation depends alone either on cortical specialisation or on growth antagonism is not to be sufficiently explicit.
2. That furrow formation depends primarily on evolutionary antagonism between the neopallium which is constantly acquiring new areas, and its fibro-osseous capsule, the skull.
3. That the furrows thus originated tend to appear at the edges of areas possessing cyto-architectural differences.
4. That in the primate brain furrow formation depends on constant factors throughout the order.
5. That the highly convoluted brains of carnivora, ungulata and cetacea argues a mode of origin different from that existing in the primates.

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THE VAGUS NERVE OF THE SNAPPING TURTLE (CHELYDRA SERPENTINA)

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From the Anatomical Laboratory of Northwestern University Medical School

NINE FIGURES

In attempting to determine the physiological significance of the unmyelinated fibers,[1] which we have found in very large numbers in the cerebrospinal nerves of mammals, it is important to have some notion of their phylogenetic position. Do they represent a system of fibers acquired in the mammalian nervous system and, therefore, phylogenetically young and correspondingly incomplete in their ontogenetic development? Such an interpretation is suggested by the delayed and incomplete myelination of the pyramidal tract (Linowiecki '14), a tract which is found only in the mammalian nervous system. The vagus nerve is well suited for a comparative study of the unmyelinated fibers of the cerebrospinal nerves, because, in the mammal, it has been shown to contain an unusually large number of these fibers distributed in a characteristic way. The vagus of the snapping turtle is of special interest because its afferent ganglion cells are grouped differently from those of the mammal. On account of this arrangement of the ganglion cells it has been possible to settle certain questions which remained obscure after the study of the mammalian vagus (Chase and Ranson '14).

Large snapping turtles were used and the study was confined to the right vagus. Most of the material was fixed and stained

[1] In a report before the Society of Normal and Pathological Physiology, Oct. 27, 1914, Professor H. H. Donaldson advocated the use of the terms myelin, myelinated and unmyelinated in the place of medulla and its derivatives in the description of nerve fibers. This new usage has been adopted throughout this paper.

in osmic acid but some was prepared by the pyridine silver technique. Except for the long stretch between the esophageal branch and the thoracoabdominal ganglion of the vagus the material was cut and mounted in serial sections.

THE RELATION OF THE ACCESSORY NERVE TO THE VAGUS

The vagus and accessory nerves are even more intimately associated with each other in reptiles than in mammals. In the turtle the accessory nerve has a separate existence only in its roots. After fusion with the vagus its fibers intermingle with those of that nerve. In the mammal the spinal part of the accessory maintains its identity as a separate fascicle throughout the common vagoaccessory trunk; but the bulbar part of the accessory fuses with, and becomes lost in the vagus nerve. In the turtle the spinal part of the accessory is very small; and its fibers, as well as those of the bulbar portion, intermingle with those of the vagus. Since in mammals we speak of the common trunk formed by the bulbar portion of the accessory and the rootlets of the vagus as the vagus nerve, we shall do least violence to the accepted terminology if we speak of the common trunk formed by the union of the roots of the vagus and accessory nerves of the turtle as the vagus nerve. It should be remembered, however, that this common trunk contains a few fibers not properly belonging to the vagus but derived from the spinal root of the accessory and given off as a minute branch to some of the neck muscles. It is generally admitted that the bulbar part of the accessory is properly to be regarded as a part of the vagus (Chase and Ranson '14).

GROSS ANATOMY OF THE VAGUS NERVE

The accessory nerve arises by four or five small rootlets from the posterior part of the lateral surface of the medulla in line with the rootlets of the vagus and by a spinal root. In one specimen studied in serial sections the spinal root was seen to arise as a single fascicle from the lower part of the second cervical segment of the spinal cord in line with the dorsal roots. In this

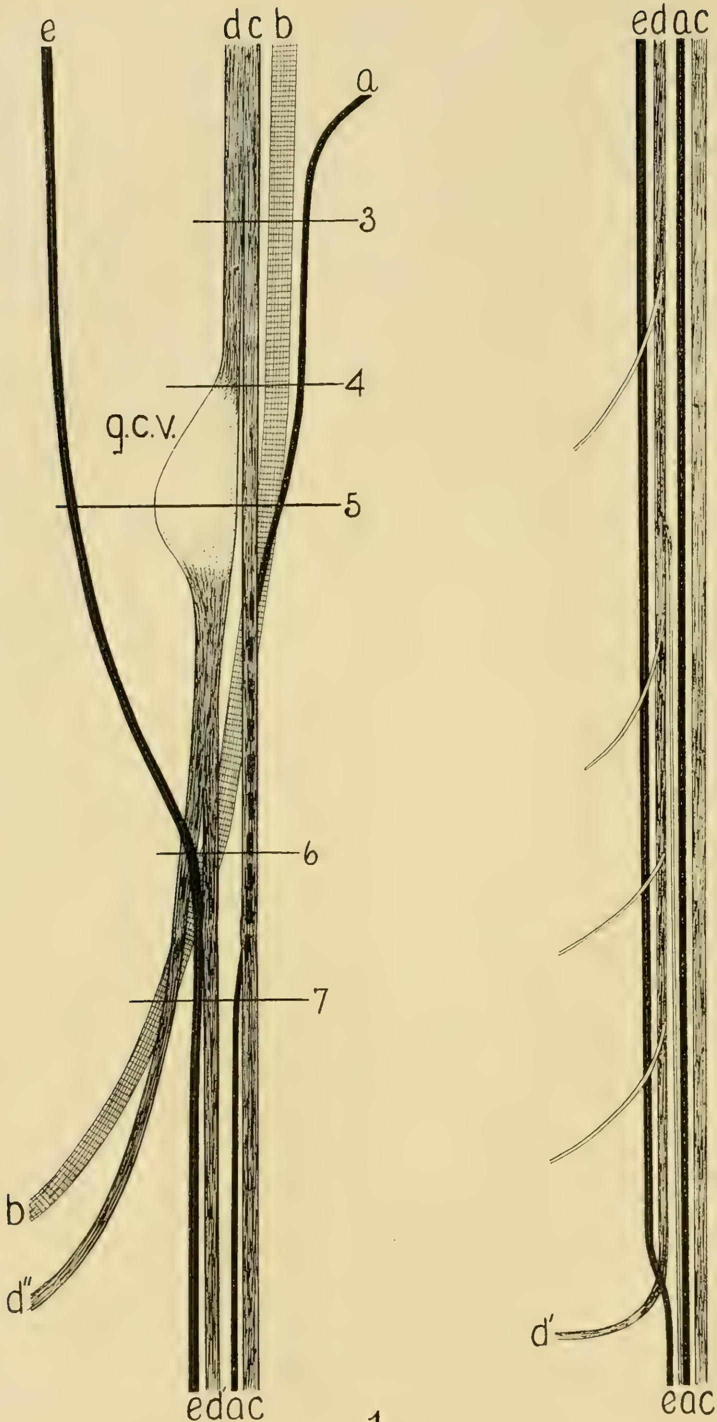
specimen both right and left spinal roots contained afferent ganglion cells. According to Weigner ('01) the accessory nerve of man also contains afferent ganglion cells.

The vagus arises by one large and two or three smaller rootlets from the posterior part of the lateral surface of the medulla. These soon unite to form a single fascicle somewhat larger than that formed by the union of the rootlets of the accessory. The two fascicles, the accessory and vagus, then run together into the jugular foramen, fuse into a single trunk, and entirely lose their individuality some distance above the cervical ganglion of the vagus.

The vagus and accessory nerves pass through the jugular foramen as a single nerve trunk, which is joined shortly after it leaves the cranium by the hypoglossal nerve (fig. 1). By careful dissecting the hypoglossal nerve may be separated from the common vagoaccessory trunk and is then seen to pass behind the vagus toward the pharyngeal wall.

The position of the more cephalad of the two ganglia of the vagus, which we shall call the ganglion cervicale vagi, differs considerably in different specimens. In three of our specimens the position and connections of this ganglion were found as shown diagrammatically in figure 1. In these three specimens the vagus divides just above the ganglion into two branches. One of these branches runs by the ganglion without forming connections with it and continues into the thoracoabdominal cavity without giving off any branches in the neck. This branch, which we shall call the ramus thoracoabdominalis, is the continuation of the vagus nerve and is directly homologous with the vagus nerve in the lower part of the neck of mammals. The other branch which is distributed entirely to structures in the neck we have called the ramus cervicalis. It divides into two branches: one of which the nervus laryngopharyngeus is distributed to the pharynx and larynx; the other the nervus esophageus runs with the thoracoabdominal ramus for some distance and is then distributed to the upper end of the esophagus.

The spinal part of the accessory is given off as a small branch in the neighborhood of the cervical ganglion. There is also a



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small communicating branch to the glossopharyngeal nerve given off at the level of this ganglion. Neither of these branches were identified in the series from which figure 1 was reconstructed.

The relations of the sympathetic trunk and the descendens hypoglossi to the vagus are well illustrated in the figures and need not be described in detail. Below the level of the laryngopharyngeal branch four nerves—the sympathetic trunk, the descendens hypoglossi, and the esophageal and thoracoabdominal branches of the vagus—are included in a single connective tissue sheath. In the lower part of the neck the esophageal branch and the descendens hypoglossi have left the common

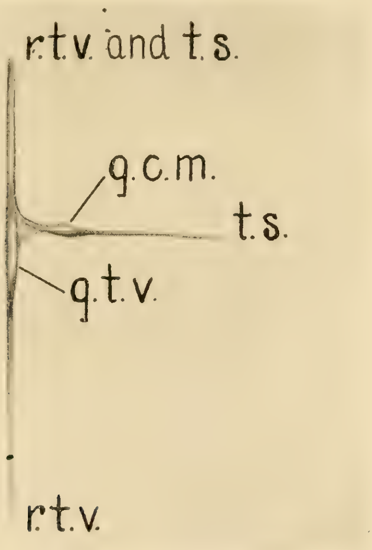

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Fig. 1 Diagrammatic reconstruction from serial sections of the upper part of the right vagus nerve in the snapping turtle. The nerve is viewed from in front with the more proximal part in the left hand figure. *a*, ramus descendens hypoglossi; *b*, N. hypoglossus; *c*, ramus thoracoabdominalis vagi; *d*, ramus cervicalis vagi; *d′*, N. esophageus; *d″*, N. laryngopharyngeus; *e*, truncus sympatheticus; *g.c.v.*, ganglion cervicale vagi.

Fig. 2 The vagus of the snapping turtle in the upper part of the thoracoabdominal cavity. *r.t.v.*, ramus thoracoabdominalis vagi; *t.s.*, truncus sympatheticus; *g.c.m.*, ganglion cervicale medium of the sympathetic trunk; *g.t.v.*, ganglion thoracoabdominale vagi.

sheath; but the sympathetic trunk and thoracoabdominal vagus run together into the thoracoabdominal cavity. Opposite one of the lowest cervical vertebrae and under cover of the plastron the sympathetic leaves the vagus and turns abruptly dorsad toward the inferior cervical ganglion of the sympathetic. At the point at which the two nerves separate there is developed on the one the middle cervical sympathetic ganglion, and on the other the ganglion thoracoabdominale vagi (fig. 2).

A short distance below the thoracic ganglion the recurrent nerve is given off and, running under the arch of the aorta, turns back along the trachea. A little farther caudad the nerve breaks up into pulmonary, cardiac and gastric rami.

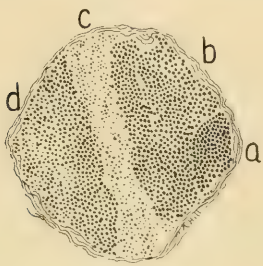
While the arrangement of the ganglia and branches of the vagus given above may be taken as typical, there is a very wide range of variation in individual specimens; especially important variations occur in the position of the cervical ganglion of the vagus which is often located higher up on the nerve before it has divided instead of on the cervical ramus. However, as three specimens were found in which the ganglion was located on, and restricted to, the cervical ramus it is safe to say that in the other cases in which it was located on the undivided trunk the ganglion really belonged to the cervical division of the nerve.

STRUCTURE OF THE VAGUS AND ITS GANGLIA

1. Roots. The rootlets of the vagus are all alike in their structure, differing in this respect from those of the dog (Chase and Ranson). The vagus rootlets of the turtle are composed of myelinated fibers of all sizes, small and medium sized ones predominating. Among the myelinated are large numbers of unmyelinated fibers. The spinal root of the accessory is formed of medium and large sized myelinated fibers. The bulbar roots of the accessory are formed of myelinated fibers of all sizes, the small ones greatly predominating. There are very few unmyelinated fibers in the rootlets of the accessory nerve.

2. The vagus nerve in the neck. As will be seen by figure 1, the vagus, accessory and hypoglossal nerves form a single nerve

trunk in the upper part of the neck, but the latter is readily distinguished as a separate fascicle in cross sections of the common nerve trunk at this level. In figure 3 the hypoglossal (*b*), and the small fascicle, the descendens hypoglossi, which the hypoglossal derives from the first cervical (*a*) are represented darker than the other fascicles of the trunk. This darker appearance in osmic sections is due to the fact that these fascicles are composed chiefly of large myelinated fibers. The descendens



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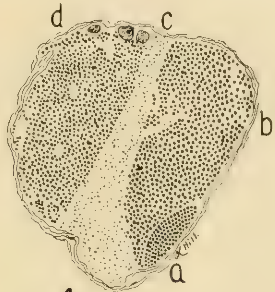

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Fig. 3 Section of the vagus and hypoglossal nerves at the level indicated by *3*, figure 1. *a*, ramus descendens hypoglossi; *b*, N. hypoglossus; *c*, ramus thoracoabdominalis vagi; *d*, ramus cervicalis vagi. Osmic acid. × 36.

Fig. 4 Section of the vagus at the level indicated by *4*, figure 1. *a*, ramus descendens hypoglossi; *b*, N. hypoglossus; *c*, ramus thoracoabdominalis vagi; *d*, ramus cervicalis vagi. Osmic acid. × 36.

hypoglossi is composed almost exclusively of large myelinated fibers, while in the hypoglossal there are a few medium and small sized ones. There also are two or three clumps of closely packed unmyelinated fibers. These resemble the bundles of sympathetic fibers in the mammalian hypoglossal (Koch, unpublished observations) and are here interpreted as such.

Above this level the vagus and accessory nerves have fused into a single trunk and lost their separate identity. The vago-accessory trunk has now divided into two well defined fascicles separated by a sharp line but not by any connective tissue septum. The lightly stained bundle (*c* in fig. 3) is the thoracoabdominal ramus of the vagus and all its fibers are destined for the thorax and abdomen. The other, more darkly stained, fascicle (*d*, fig. 3) is the cervical ramus of the vagus, and all its fibers end in structures in the neck. These fascicles differ

greatly from each other in structure. The cervical ramus contains myelinated fibers of all sizes about equally mixed together, scattered among which there are found a relatively small number of unmyelinated fibers. The thoracoabdominal ramus is composed chiefly of unmyelinated fibers among which are scattered myelinated fibers of all sizes. Of the myelinated fibers the majority are small. It is the preponderance of unmyelinated fibers that gives this fascicle its light appearance in osmic acid preparations.

These points concerning the structure of the various fascicles have been determined from a study of sections stained with osmic acid, showing the myelin sheaths, and others stained by the pyridine silver method, showing the axons. A comparison of the two kinds of sections shows that the thoracoabdominal ramus of the vagus is composed of great numbers of axons, most of which are very slender, while it contains only scattering myelin sheaths. Some very instructive preparations were obtained with osmic acid. In these preparations the myelin sheaths are deep black and readily recognized as such on the smallest myelinated axons. Some of these myelinated axons are even smaller than the average unmyelinated ones and yet their myelin sheaths are perfectly distinct. Connective tissue and neurilemma stain a light yellow, while all the axons are colorless. In such preparations one can readily recognize the unmyelinated fibers (fig. 8). The colorless axons are encircled by a light yellow neurilemma ring. This yellow ring contains no trace of black myelin. The unmyelinated fibers in the sympathetic trunk of the turtle have an exactly similar appearance in good osmic acid preparations. Somewhat similar appearances were noted in the mammalian vagus; but in osmic acid preparations of the dog's vagus the individual unmyelinated fibers do not stand out with anything like the same clearness. In the dog's vagus the tissue separating the myelinated fibers has when highly magnified a 'reticulated' appearance (Chase and Ranson '14).

Figure 4 shows the same bundles in slightly different arrangement at the level of the highest part of the cervical ganglion.

The cervical ramus at this level contains a few ganglion cells and serial sections show that all the cells of the superior ganglion are contained in this division of the nerve. At a somewhat lower level, figure 5, the cervical ramus with its ganglion has become separated from the vago-hypoglossal trunk by a connective tissue septum. The thoracoabdominal ramus of the vagus (*c*) remains free from ganglion cells. All the fascicles, except the cervical ramus of the vagus, present at this level the same structure as at higher levels. Another nerve enters

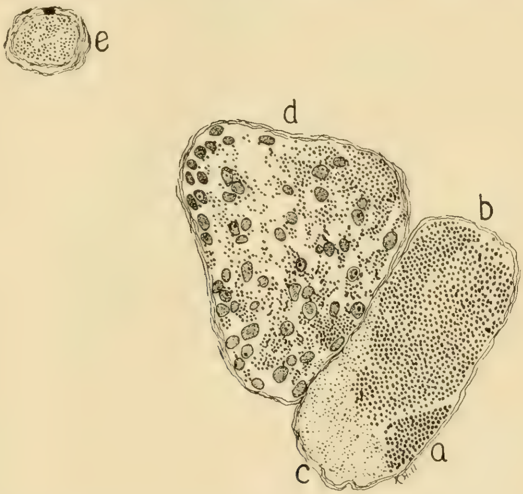


Fig. 5 Section of the vagus at the level indicated by *5*, figure 1. *a*, ramus descendens hypoglossi; *b*, N. hypoglossus; *c*, ramus thoracoabdominalis vagi; *d*, ramus cervicalis vagi with the ganglion cervicale vagi; *e*, truncus sympatheticus. Osmic acid. × 36.

the series at this point (fig. 5, *e*). It is the sympathetic trunk and has the same structure as the thoracoabdominal ramus of the vagus, except that its myelinated fibers are all small. These two nerves have about the same proportion of myelinated and unmyelinated fibers.

Figure 6 is taken some distance below the ganglion. At this level the thoracoabdominal ramus of the vagus (*c*) accompanied by the descendens hypoglossi (*a*) has separated somewhat from the other fascicles of the common trunk. The cervical ramus

of the vagus has divided into the laryngopharyngeal (d'') and the esophageal branch (d') and in the angle between these branches lies the sympathetic trunk (e). After the laryngopharyngeal branch has separated from the esophageal branch the sympathetic trunk runs with the latter (d', e, fig. 7). The

Fig. 6 Section of the vagus at the level indicated by *6*, figure 1. *a*, ramus descendens hypoglossi; *b*, N. hypoglossus; *c*, ramus thoracoabdominalis vagi; d', N. esophageus; d'', N. laryngopharyngeus; *e*, truncus sympatheticus. Osmic acid. × 36.

thoracoabdominal ramus and esophageal branch of the vagus, the descendens hypoglossi and the sympathetic trunk all run caudad in a common sheath.

3. The vagus nerve in the thoracoabdominal cavity. The esophageal branch and the descendens hypoglossi leave the vagus in the neck, but the sympathetic trunk and the thoracoabdominal vagus occupy the same sheath as they lie ventro-lateral to the lower cervical vertebrae under the plastron. Here they each develop a ganglion, the middle cervical ganglion of the sympathetic and the thoracoabdominal ganglion of the vagus (fig. 2). Serial sections show that the two nerves, though contained in a common sheath, are separated by a connective tissue septum.

The ganglia are also entirely separate. There are a few very minute and one fair sized communicating branch between the two nerves in this position. The cells in the thoracoabdominal

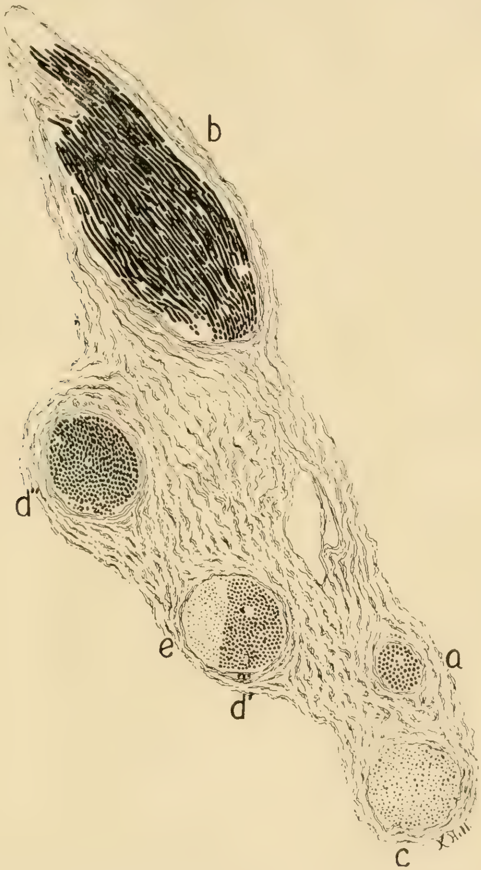


Fig. 7 Section of the vagus at the level indicated by 7, figure 1. *a*, ramus descendens hypoglossi; *b*, N. hypoglossus; *c*, ramus thoracoabdominalis vagi; *d'*, N. esophageus; *d''*, N. laryngopharyngeus; *e*, truncus sympatheticus. Osmic acid. × 36.

ganglion of the vagus are distributed along the nerve for some distance, so that the ganglion although of good size does not produce much of an enlargement on the nerve.

It is of special interest that the structure of the thoracoabdominal ramus is the same at all levels. It is the same high

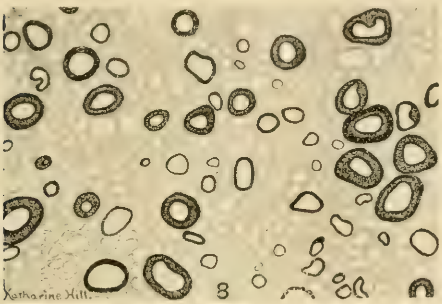
in the neck as it is below the level of the thoracoabdominal ganglion. No change has taken place in the proportion of myelinated and unmyelinated fibers. This speaks against the possibility of myelinated fibers losing their sheaths during their course and thus becoming unmyelinated fibers. It would also indicate that the thoracoabdominal ganglion was in no part sympathetic. But we will take up these points in another place.

The recurrent nerve is given off just before the vagus breaks up into pulmonary gastric and cardiac branches. It is a well myelinated nerve consisting chiefly of small and medium sized myelinated fibers with a few large myelinated ones and some unmyelinated axons. The pulmonary rami contain a slightly larger proportion of the myelinated fibers than do the gastric rami. Most of the larger myelinated fibers in the vagus below the recurrent nerve enter the pulmonary rami. Both the pulmonary and gastric rami are rich in unmyelinated fibers. The cardiac rami could not be identified in the sections.

4. The ganglia in the vagus nerve. The cervical ganglion of the vagus is associated exclusively with the cervical ramus as is shown by a study of serial sections through the vagus from which figure 1 was reconstructed. The ganglion was found in the same position in two other series. In still other series the ganglion was found higher up on the undivided trunk, but we may assume that in these cases also the cells were associated only with fibers destined for the cervical ramus. The inferior ganglion is associated only with the fibers which enter the thorax. These two ganglia are not strictly homologous to the jugular and nodose ganglia of mammals. According to Molhant ('13) the nodose ganglion contains most of the cells of origin of the sensory fibers to the larynx, and all of those of the sensory fibers to the esophagus, trachea, heart, lungs and stomach. The thoracoabdominal ganglion of the turtle differs from the nodose ganglion of mammals in that none of its cells are associated with laryngeal fibers. In other words, the mammalian nodose ganglion corresponds to the thoracoabdominal and part of the cervical ganglion of the turtle.

Almost all the cells, especially in the cervical ganglion, possess protoplasmic processes ending in end bulbs. Some are very

fine, others coarse and the terminal bulbs vary greatly in size (fig. 9). Arising from some of the axons are to be seen collaterals with terminal bulbs. Especially in the thoracoabdominal ganglion many axons were split up near their origin into complicated



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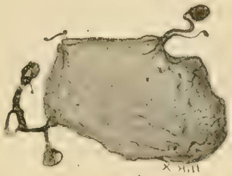

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Fig. 8 A small area of the thoracoabdominal ramus of the vagus at the level indicated by *4*, figure 1, showing the myelin sheaths of the myelinated fibers as black rings and the neurilemma of the unmyelinated fibers as just visible rings which in the preparations are of the same tone of yellow as the connective tissue. Osmic acid. × 955.

Fig. 9 A cell from the cervical ganglion of the vagus showing protoplasmic processes with end bulbs. Pyridine silver. × 955.

plexuses similar to those described by Dogiel ('08), Ranson ('12) and others in mammalian cerebrospinal ganglia. But the sections were not thick enough to include more than a part of a plexiform axon in a single section and the details of these plexuses could not be readily worked out from serial sections.

THEORETICAL CONSIDERATIONS

1. In the mammal Chase and Ranson showed that the vagus nerve contains a very great number of unmyelinated fibers. Most of the large myelinated fibers leave the vagus through its cervical branches, while the majority of the unmyelinated fibers run downward in the main trunk to be given off in the thoracic and abdominal branches. The proportion of myelinated and unmyelinated fibers in the turtle's vagus is approximately the same as in that of the dog; and in both animals we find the myelinated fibers chiefly distributed in the cervical branches, while most of the unmyelinated fibers are distributed

through its thoracoabdominal branches. This would indicate that the unmyelinated fibers do not represent a recently acquired group of fibers in the mammalian nervous system, but that they are present in lower vertebrates in about the same proportion and distributed in the same way as in the mammals. It would seem that the distinction between the two kinds of fibers is a fundamental one. The unmyelinated fibers of the cerebrospinal nerves do not form a phylogenetically young system and the incompleteness of their ontogenetic development (i.e., their failure to develop a myelin sheath) must find some other explanation.

2. In the mammalian vagus it was found that the relative proportion of unmyelinated fibers increases rapidly from above downward, at least in the region of the jugular and nodose ganglia where the cervical branches are given off. Most of this change in the relative proportion of the two kinds of fibers was considered due to the cervical branches taking out almost nothing but myelinated fibers, leaving behind an increasing proportion of unmyelinated fibers. But it was considered possible that the preganglionic visceral efferent fibers of the vagus might lose their sheaths in their course down the vagus, myelinated being thus transformed into unmyelinated fibers. This possibility has been definitely ruled out by the study of the turtle's vagus. The fibers destined for the thoracoabdominal viscera separate all at once into a well defined nerve trunk, just below the base of the cranium. This trunk has the same structure as the thoracic vagus of the mammal and it retains this same structure throughout the neck. There is no increase in the proportion of unmyelinated fibers from the place where the cervical ramus splits off to the point of origin of the recurrent nerve in the thoracoabdominal cavity. The preganglionic myelinated fibers of the turtle's vagus do not to any appreciable extent lose their myelin sheaths during their course down the vagus.

3. It was also possible that some of the unmyelinated fibers of the mammalian vagus were post ganglionic visceral efferent fibers arising from sympathetic cells in the jugular and nodose ganglia. Although such an assumption would have helped

explain the increasing proportion of unmyelinated fibers found in serial sections as one passed from above downward through the region of the two ganglia, it was considered very improbable that the unmyelinated fibers of the vagus were to any considerable extent postganglionic visceral efferent fibers. The work on the turtle shows clearly that none of them can be so considered, since there are no ganglion cells in the thoracoabdominal ramus in the neck and yet this branch contains as many unmyelinated fibers as the thoracic trunk of the vagus in the dog. None of these fibers have been in contact with peripheral ganglion cells and they cannot therefore be postganglionic sympathetic fibers. Since there is no appreciable change in the myelination of the vagus above and below the thoracoabdominal ganglion, it is probable that there are no sympathetic elements in this ganglion.

CONCLUSIONS

1. The vagus of the turtle divides high in the neck into a cervical and a thoracoabdominal ramus.

2. The cervical ramus is composed almost entirely of myelinated fibers and the cells of the cervical ganglion of the vagus are associated with the fibers of this ramus only.

3. The thoracoabdominal ramus is composed chiefly of unmyelinated fibers among which are scattered myelinated fibers. It presents as it passes under the plastron an enlargement, the thoracoabdominal ganglion, the cells of which are associated with the fibers of this ramus only.

4. The unmyelinated fibers are present in about the same proportion and distributed in the same way in the vagus of the turtle as in that of the mammal.

5. The unmyelinated fibers in the vagus are not postganglionic visceral efferent fibers arising from sympathetic cells in the ganglia of that nerve.

6. The preganglionic visceral efferent fibers of the vagus do not become transformed into unmyelinated fibers in their course down the vagus.

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A FURTHER CONTRIBUTION TO A KNOWLEDGE OF THE LATERAL LINE SYSTEM IN EXTINCT AMPHIBIA

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SEVEN FIGURES

Since the publication of an earlier paper[1] on the occurrence of the lateral line organs in extinct Amphibia, in which was given a complete bibliography of the subject up to that time, there have been several interesting additions to our knowledge of these important organs as they occur among the primitive land vertebrates, in the remains which have so far been secured. These results are contained in contributions by Wiman ('14), Fraas ('13), Williston and the writer ('13), and have been briefly reviewed elsewhere.[2] It is the intention here to collect these observations into one place in an attempt to correlate the canals, as they occur in the extinct Amphibia, with what is known from the fishes, and to that end the work of McMurrich ('84), Herrick ('01), Pfüller ('14) and others are noted; and the possible importance of their results to the elucidation of the anatomy of the early land vertebrates is discussed.

One of the most interesting observations on the occurrence of the lateral line organs in the extinct Amphibia has recently been given me by Doctor Williston, and I have his permission to use his results in this place. Among the Permian Amphibia of North America, there are three types of skulls exhibited. Many species show no trace of the lateral line canals on the skull,

[1] Jour. Morph., vol. 19, no. 2, pp. 511–540, figs. 1–17, bibliography, 1908.
[2] Amer. Nat., vol. 49, June, pp. 369–376, 1915.

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such as Trematops, and Cacops.[3] Some, such as Eryops[4] and Diplocaulus, have imperfectly developed lateral line canals, in the form of interrupted, shallow grooves, and others such as Trimerorhachis[5] have the lateral line canals sharply incised. Doctor Williston suggests therefore that the group represented by Trematops and Cacops are purely land-living amphibians. Eryops and Diplocaulus are transitional types which live partly in, partly out of, water and that Trimerorhachis is a strictly aquatic type. With the aquatic habit in Trimerorhachis goes a peculiarly interesting development of the pectoral girdle which is very like the pectoral girdle of the large labyrinthodonts, Mastodonsaurus,[6] and its allies.

This observation of Williston's agrees well with those of Kingsbury[7] on the temporary loss of the lateral line organs in Diemyctylus on leaving the water for breeding purposes. It also agrees well with the loss of lateral line organs in the metamorphosis of the tadpole of the frog and in Salamandra.

If the occurrence of lateral line organs indicates an aquatic habit for the animals possessing them, as seems entirely possible, then the fauna described by Wiman ('14) is aquatic, for the lateral line canals are unusually distinct and with this sharp incision of the lateral line canals goes a pectoral girdle consisting of corrugated clavicles and interclavicles which is entirely similar to the same elements in Mastodonsaurus and Trimerorhachis. The species described by Wiman are all new and in view of the im-

[3] Trematops: Jour. Geol., vol. 17, no. 7, pp. 636–658, figs. 1–6, 1909; Cacops: Bull. Geol. Soc. Amer., vol. 21, pp. 249–284, pls. 6–17, 1910. See also: Revision of the Amphibia and Pisces of the Permian of North America. Publication No. 146, Carnegie Institution of Washington, 1911; Jour. Geol., vol. 22, no. 1, pp. 57–70, figs. 1–11, 1914.

[4] Jour. Morph., vol. 19, no. 2, pp. 521–525, figs. 9–11, 1908; ibid., vol. 23, no. 1, pp. 31–43, pls. 1–2, 1912; Revision of the Amphibia and Pisces of the Permian of North America, by E. C. Case, publ. 146, Carnegie Inst., pp. 15–31, pls. 1–10, 1911; Transactions Kansas Academy Science, 1909.

[5] Jour. Geol., vol. 21, no. 7, pp. 625–627, 1 fig., 1913.

[6] Paleontographica, Bd. 36, pp. 1–158, pls. 1–17, 1889; ibid, Bd. 60, pp. 275–294, Tafln. 16–22, 1913.; Führer durch das kgl. Naturalien-Kabinett zu Stuttgart, 1906, by E. Fraas.

[7] Proceedings Amer. Microscop. Soc., vol. 17, p. 130, 1895.

portance of the lateral line canals in vertebrate morphology it is thought worth while to copy a few of Wiman's figures and attempt to correlate the lateral line canals in these new forms with the work which has previously been done.

The canals as they occur on the skull of Lyrocephalus euri Wiman (fig. 1) are broad but perfectly distinct grooves which have the arrangement indicated in figure 1. By 'Nasofrontalkanäle' I presume Wiman means the supraorbital (fig. 1, *So*). He says that this canal varies in different individuals so that some specimens exhibit the canal twice the breadth of others. Wiman remarks further that "Der Verlauf der Schleimkanäle ist wie überhaupt bei wenigstens den höheren Stegocephalen auffallend konstant" but there are certain very interesting deviations from the usual condition. There is to be noted in the figures an asymmetrical arrangement of the canals in all of the forms figured. This asymmetry is especially apparent in the temporal region.

The supraorbital canal (figs. 1, 2, 4, *So*) has a course running nearly the entire length of the skull; and at the posterior projection (fig. 1, *X*) the canal was probably elevated into the skin and made no impression on the skull bones. On the post-orbital bone the supra-orbital canal is joined by a branch from the temporal and jugal which may be looked upon as an extension of the hyomandibular canal which in turn runs down on to the mandible as the homologue of the operculo-mandibular of Amia (Allis '89). There are various anomalies associated with the supraorbital canals. In one skull (Wiman '14, pl. 1, fig. 1) the canals end abruptly at some distance from the ascending hyomandibular. On another skull the temporal canal fails to join the supraorbital canal. Yet again the canal of one side may join the ascending branch and on the other be present in the form of a very slight groove or represented by a row of pits (fig. 4) which doubtless contained the sensory organs.

The 'Tremalkanäle' of Wiman are the canals which have been termed temporal (Moodie '08, p. 514, fig. 1) and probably represent a backward extension of the hyomandibular or else a new formation in the Amphibia. The occurrence of the tem-

poral canal is very similar in the species figured by Wiman. In one species, Lonchorhychus öbergi Wiman, there is a peculiar medial projection (fig. 4, *b*) which is asymmetrically developed.

Wiman refers to the canals occurring on the squamosal and jugal as the 'temporal-Kanäle.' They are either the anterior portion of the operculo-mandibular canal or the posterior part of the infraorbital (*i.o.*). For the sake of convenience the present writer has previously referred to them as jugal canal ('08, p. 515, fig. 1). Wiman seems not to have been aware of this paper.

The 'Maxillarkanal' of Wiman is the infraorbital of other writers. It has a uniform course in the various skulls figured. Its entire course is shown in figure 3 (*i.o.*) which represents its occurrence in Lonchorhynchus öbergi Wiman.

On another skull figured by Wiman ('14, pl. 5, fig. 1), that of Aphaneramma rostratum Woodward, the canals have a most unusual arrangement. The unequal supraorbital canals do not extend posterior to the orbits which are far forward; the temporal canal is extensive and runs down on the side of the skull to join the jugal. The projection is on one side a crescent far removed

Fig. 1 Superior view of the skull of Lyrocephalus euri, Wiman, from the Triassic of Spitzbergen. After Wiman ('14).

a.c., anterior commissure; *f.*, frontal bone; *hy.*, hyomandibular junction of the canals of skull and mandible; *i.o.*, infraorbital lateral line canal; *j.*, jugal canal; *j'.*, jugal bone; *n*, nostril; *or.*, orbit; *p.*, parietal bone; *pf.*, parietal (pineal) foramen; *p.o.*, postorbital; *pp.*, postparietal; *p.r.f.*, prefrontal+lachrymal; *s.o.*, supraorbital lateral line canal; *sq.*, squamosal; *st*, supratemporal; *t.*, temporal canal; *x.*, posterior extension of supraorbital canal.

Fig. 2 Superior view of the skull of Lonchorhynchus öbergi, Wiman, from the Triassic of Spitzbergen. After Wiman ('14).

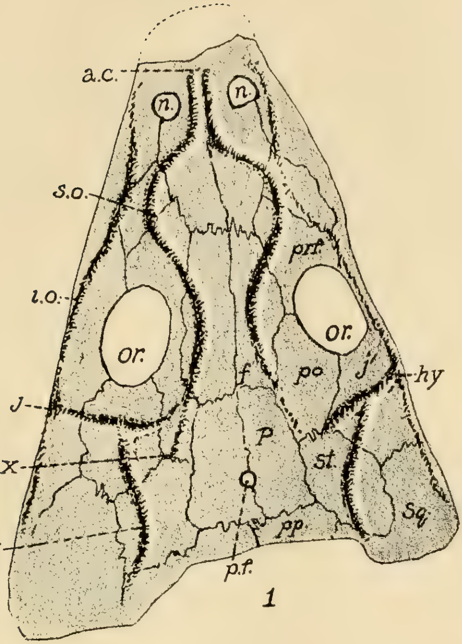
b., aberrant extension of the jugal canal (fig. 4); *i.o.*, infraorbital lateral line canal; *j.*, jugal canal; *or.*, orbit; *s.o.*, supraorbital lateral line canal; *t.*, temporal canal.

Fig. 3 Lateral view of the skull of Lonchorhynchus öbergi, Wiman, from the Triassic of Spitzbergen. After Wiman ('14).

b., aberrant bud from the jugal canal; *i.o.*, infraorbital canal. *or.*, orbit; *t.*, temporal canal.

Fig. 4 Dorsal view of the skull of Lonchorhynchus öbergi, Wiman. From the Triassic of Spitzbergen. After Wiman, ('14).

b., aberrant bud from the jugal canal; *or.*, orbit; *p.o.*, pineal opening; *s.o.*, supraorbital lateral line canal; *t.*, temporal lateral line canal.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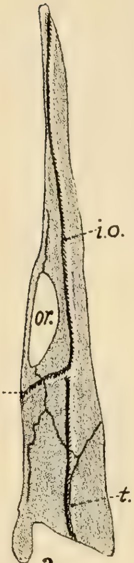
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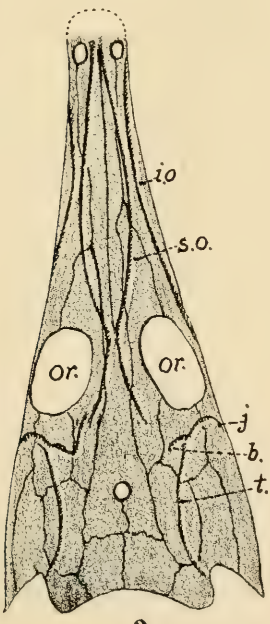
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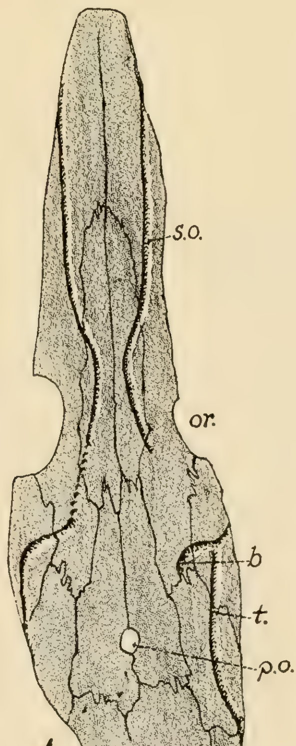
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from the temporal canal, and on the other quite horseshoe-shaped and nearly connected with the temporal canal.

It will be seen from an examination of the figures (1–4) that the parietal foramen is large and clearly marked. It has always been assumed that this opening was for the pineal organ. There are surely some fortunate casts of the cranial cavity of an extinct amphibian in some of the extensive collections of fossil vertebrates, which will show that part of the brain; and it is to be hoped that some one will describe the condition of this part of amphibian anatomy in its relation to the skull.

Micrerpeton caudatum[8] was the first branchiosaurian described from the western hemisphere and the species was found to be especially interesting in the preservation on the tail of two dark lines which have been interpreted as dorsal and median lateral lines.[9] This observation has been confirmed on additional material (fig. 5) from the same deposit on three specimens which have been assigned to another genus, of which the writer[10] has already described the anatomy.

A reconstruction of the form is here given (fig. 6), the median and dorsal lateral lines of the tail being indicated as dark bands. In the description of Micrerpeton the writer[11] discussed the presence of small scales on the side of the tail impression, and stated that the lateral line organs seemed to have been located under pigmented scales, to which was due the preservation of the form of this series of organs. The material on which the reconstruction is based consists of three unusually well-preserved specimens (fig. 5), of a small amphibian less than two inches in length. All three specimens show a nearly complete preservation of the alimentary canal, the pigementum nigrum of the iris and choroid, the form of the body, something of the skeleton, and the lateral line organs, above mentioned. The form [12] is very closely

[8] Jour. Geol., vol. 17, pp. 39–52, figs. 1–6, 1909.

[9] Jour. Morph., vol. 19, p. 517, figs. 4–5, 1908.

[10] Kansas Univ. Sci. Bull., vol. 6, no. 2, p. 331, pl. 6, fig. 2, 1913; Amer. Natl., vol. 44, p. 367, figs. 1–4, 1910.

[11] Jour. Geol., vol. 17, p. 49, fig. 6, 1909.

[12] Fortschritte d. naturwissenschtl. Forschung, Halle, Bd. 8, p. 66, fig. 35, 1913.

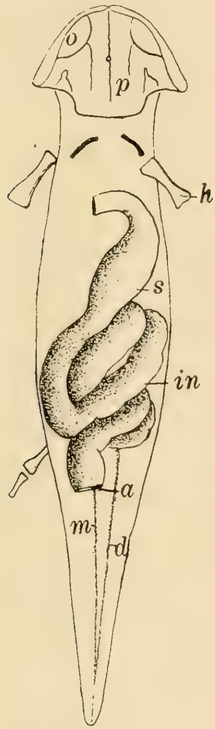

Fig. 5 Drawing of a specimen of a Coal Measures branchiosaurian, Eumicrerpeton parvum Moodie, from the Illinois, Mazon Creek beds; showing the preservation of the lateral line sense organs on the tail; the nearly complete alimentary tract, and the outline of the body. × 2.

a., anus; *d.*, dorsal lateral line of tail; *h.*, humerus; *in.*, intestine; *m.*, median lateral line series of the tail; *o.*, orbit; *p.*, parietal bone; *s.*, stomach.

related to Branchiosaurus of Europe and a few details from the European genus are used in the reconstruction of this Coal Measures salamander. The form of the body was modeled in wax and the drawing was made by Mr. Tom Jones from this model (fig. 6).

In the discussion of the three specimens of Eumicrerpeton[13] it was stated that:

> The impression of the larger animal, which is probably an adult, presents * * * * * the entire impression of the tail, on which,

[13] Kansas Univ. Sci. Bull., vol. 6, no. 2, p. 331, 1913.

as in Micrerpeton caudatum Moodie, there occur two definite dark lines, one beginning at the tip of the tail and running obliquely along the tail to where the impression is broken at the anal region; the other beginning at a distance of four and one-half millimeters from the tip and running almost parallel with the median line. These two lines undoubtedly represent the lateral line system (figs. 5 and 6).

Fig. 6 A reconstruction of the possible appearance in life of the Coal Measures branchiosaurian, Eumicrerpeton parvum, a small primitive salamander less than two inches in length. The drawing is based on three well preserved specimens, showing impressions of the full form of the body and on the studies of Credner, Thevenin, Fritsch, von Ammon and Broili of the European Branchiosauria. The lateral line canals are represented as dark bands on the caudal region. The sense organs were situated beneath specialized pigmented scales and to these is due the preservation of these organs.

Fraas ('13) has described additional cranial portions of new labyrinthodonts (fig. 7) from the Triassic of Germany, which support and verify his former[14] findings of the lateral line canals

[14] Paleontographica, Bd. 36, pp. 1–156, pls. 1–18, 1889.

Fig. 7 Fraas' conception of the appearance in life of one of the gigantic labyrinthodonts, Mastodonsaurus giganteus, from the Triassic of Germany. The family represented by this animal constituted the largest forms of all known Amphibia with a maximum length of eighteen feet. They had a wide distribution but a short geological range, as our knowledge at present indicates. The figure is introduced here to give an idea of the possible appearance of the lateral line canals, on the animal when alive. Possibly they have been too prominently represented; but in the skulls studied by Doctor Fraas the lateral line grooves were broad deep furrows, cut very sharply into the facial bones. After Fraas.

in these forms. One very peculiar form is described in this new paper, Plagiosternum pulcherrimum, which has a remarkably frog-like skull. Another indication of the change to a land habitat is the nearly complete loss of the lateral line canals. The supraorbital canals are faintly indicated medially to the enormous orbits, but the other canals seem to have been lost. The pectoral girdle, so far as it is preserved, is of the aquatic type, typical of the large majority of the Labyrinthodontidae.

It has been well known for some time that the lateral line canals have, among the fishes, a very definite effect upon the location of the various peripheral osseous elements of the cranium. Some of the bones are supposed to develop in response to a stimulus from the lateral line canals and are first formed as ossicles around and in response to the development of these canals.

McMurrich ('84, p. 279) observed this some years ago in the catfish, and in his discussion he states:

In a young Amiurus, about 20 mm. in length, it was to be noticed that wherever a mucous canal appeared in transverse section a ring of bone surrounded and protected it, so that each of these canals in the cranium was surrounded by an osseous tube. The bone was apparently deposited in membrane, and was evidently formed solely for the protection of the mucous canal. In certain cases a bone, usually perforated for the emission of a branch from the canal to a pore, became formed by a lateral extension of this osseous tube into the adjacent connective tissue. Instances of such bones are the infraorbital chain, the adnasals (lachrymals) and nasals.

Similar observations have been made by Herrick ('01, p. 224):

A detailed comparison of the lateral lines of Ameiurus and the siluroids described by Pollard * * * * * brings out very clearly the peculiar and intimate relation existing between the canals and the dermal bones of the skull, a relation which has been recently emphasized by several writers. It is manifest that many of the bones, such as the extra-scapular and the suborbital series, have been developed for the canals. Conversely, it is equally evident that the canal is to a large extent dependent (probably as a cenogenetic adaptation) upon the bones and tends to disappear in their absence, as in the case of the infraorbital line of Menidia. This relation between canals and bones is, however, not an inflexible one, as evidenced for example, by the fact

that, even among the siluroids, the supraorbital and infraorbital canals may separate either in the frontal or in the post-frontal, and still more clearly by the presence of a canal and a sense organ in the inter-operculum, as well as the preoperculum. * * * * Moreover in cases where the dermal skeleton is greatly reduced, while the sensory organs of the lateral line system do not suffer a corresponding reduction, as in Lophius, the canals disappear and the courses of the lateral lines, as indicated by the rows of naked sense organs, cease to be dependent upon the positions of the underlying bones." And further he remarks: "It should be noted, however, that all lateral line ossicles are dermal bones specialized for this purpose, and that the canals do not penetrate the bones belonging to the primordial cranium. * * * * (Herrick, '01, p. 239).

The value of these observations upon any attempted correlation of the cranial elements of the fishes and Amphibia, such as has been attempted by several authors, is at once evident. If the lateral line canals control the developing cranial elements, any correlation which does not take into consideration the lateral line system is superficial. In an attempt at correlating the elements of the temporal region, the writer has already ('08) referred to the importance of the relation of the lateral line canals of the head and the cranial elements. The bones of the skull of the ancient Amphibia are all dermal and lay upon the primordial chondrocranium, with the possible exception of the bones bounding the brain case, and even these seem largely *cartilaginous.* Broom remarks[15] that the inner ear of the labyrinthodonts was contained in cartilage.

It is certain, that there is a high degree of similarity in arrangement in the peripheral osseous elements of fishes and amphibians. Whether the lateral line canals are the primary or secondary element is a matter that will have to be experimentally determined. It is an interesting fact, however, that in the more mature phyla the osseous elements retain their relative position, in the absence of the lateral line canals; but canals are only wanting in the higher and more specialized forms after the osseous elements may have become fixed by the lateral line canals, and after the sense organs have disappeared from the grooves in the

[15] Bull. Amer. Museum Natl. History, vol. 32, art. 38, p. 574, 1913.

skulls and occur only as cutaneous structures.[16] It is probably this latter condition which obtained in the young of Trematops and Cacops.

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[16] Of course, in this statement it is not intended to imply that the lateral line canals arose earlier in the phylogeny than naked lateral line sense organs. The converse is probably true, for the canals are lacking in cyclostomes, though naked sense organs of this system are present. In the terminal phyla of the Ichthyopsida the lateralis system is undergoing reduction and a return to the most primitive condition of naked sense organs.

A STUDY OF THE ENDOCRANIAL CASTS OF OCAPIA, GIRAFFA AND SAMOTHERIUM, WITH SPECIAL REFERENCE TO THE CONVOLUTIONAL PATTERN IN THE FAMILY OF GIRAFFIDAE

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TWENTY-FIVE FIGURES

INTRODUCTION

While the skeletal parts and especially the skulls of the okapi and giraffe have been carefully examined and compared in detail in the effort to determine the relationship of these living forms to one another and to the fossil Giraffidae, no attempt has been made to utilize such evidence as may be gleaned from a study of the endocranial casts.

In the present paper an effort has been made to place such data upon record in a more detailed fashion than was possible in the preliminary notes published as an abstract in the Proceedings of the American Association of Anatomists, December, 1914 (3).

The superficial convolutional pattern of the convex surface of the cerebrum in many of the lower gyrencephalous Mammalia is quite accurately reproduced by the corresponding irregularities upon the internal surface of the skull. This is especially the case,

for example, among the ungulates which I have studied in the preparation of this paper.

It is of interest to note in this connection that, in the skulls of gyrencephalous mammals of the sub-order Anthropoidea, the juga cerebralia and impressiones digitatae are much less evident than in the forms about to be described, while in man the value of endocranial markings in the determination of convolutional pattern has recently been seriously questioned (28).

Various factors must contribute to produce these different types of skull growth which are characteristic of different mammalian orders, and it would be irrelevant here to discuss this interesting question in any detail. However, as I have elsewhere mentioned, there can be no doubt that among the factors which combine to cause the condition obtaining in ungulates, the following, more especially the second, are most important: (a) the habitual position of the head in relation to the action of gravity and (b), the early maturation of growth processes in the encephalic portion of the skull.

With regard to my material, I wish to make again the following acknowledgments.

One endocranial cast of an adult okapi and one of an adult giraffe were obtained in Manchester through the courtesy of Prof. G. Elliot Smith, upon whose advice this study was undertaken. The second specimen from an adult okapi together with that from Samotherium was obtained through the courtesy of Dr. Smith Woodward from the Museum of Natural History at South Kensington, London. I am indebted also to Prof. Arthur Keith for the opportunity of studying the giraffe brains in the Museum of the Royal College of Surgeons, and to Dr. C. U. Ariëns Kappers for the like privilege of studying the ungulate and other material in the collection of the Central Dutch Institute for Brain Research in Amsterdam.

To Prof. Elliot Smith and Dr. Ariëns Kappers, I am further indebted for the helpful criticism of my earlier report.

DESCRIPTION OF SPECIMENS

(a) *Giraffa camelopardalis* (*figures 1 to 3 and 17 to 19*)

As the morphology of the giraffe brain is well known through the work of Krueg (22), Elliot Smith (9) and others, and the osteology of the skull has received special attention in the memoirs of Sir Ray Lankester (23 and 24) and Julien Fraipont (17), this cast affords excellent material upon which to begin the present study.

Only a few accurate observations upon the weight of the brain and the total body weight of the giraffe have been recorded. I quote the following figures from Max Weber (29).

		Body Weight	*Brain Weight*	*Ratio*
(1)	Male, two months old....	150,000 grams	389 grams	1: 392
(2)	Male, young adult........	300,000 grams	420 grams	1: 761
(3)	Male, adult..............	529,000 grams	680 grams	1: 777

The volume of the cast described here is 650 cc., but no record as to the total body weight of this specimen could be obtained. Taking it for granted that the specific gravity of nervous tissue in the giraffe is but little different from that in man, the approximate calculated weight of this brain would be 575 grams.

A study of the data recorded by Weber for the giraffe and of the ratios which obtain between the brain and body weight in the horse as cited by Flatau and Jacobson (12[1]), makes it evident that, in these two species the relationship of brain weight to body weight is approximately the same in adult animals of equal bulk.

The transverse diameter of the cast is greatest in the parietal region, where it measures 116 mm. across. From the basi-

[1] The further statement of these authors (l.c., p. 527) that the volume of the brain compared with that of the skull is lower among ungulates than in any other group of mammals is of interest. In this heterogeneous group the ratio varies from 1 : 7 in the horse up to 1: 10 in the elephant. This phenomenon may be correlated to some extent with the presence in certain members of the group of heavy defensive head appendages. However, it is much more probably the direct result of the herbivorous habit common to all these animals, which has given rise to the acquisition of a complicated dental mechanism and *pari passu* along with this, a facial development for its accommodation.

occipital or pontine surface to the highest point over the vermis the measurement is 70 mm. From the frontal to the occipital pole of the cerebrum the maximum length is 120 mm. The greatest diameter between the floccular areas of the cerebellum is 57 mm.

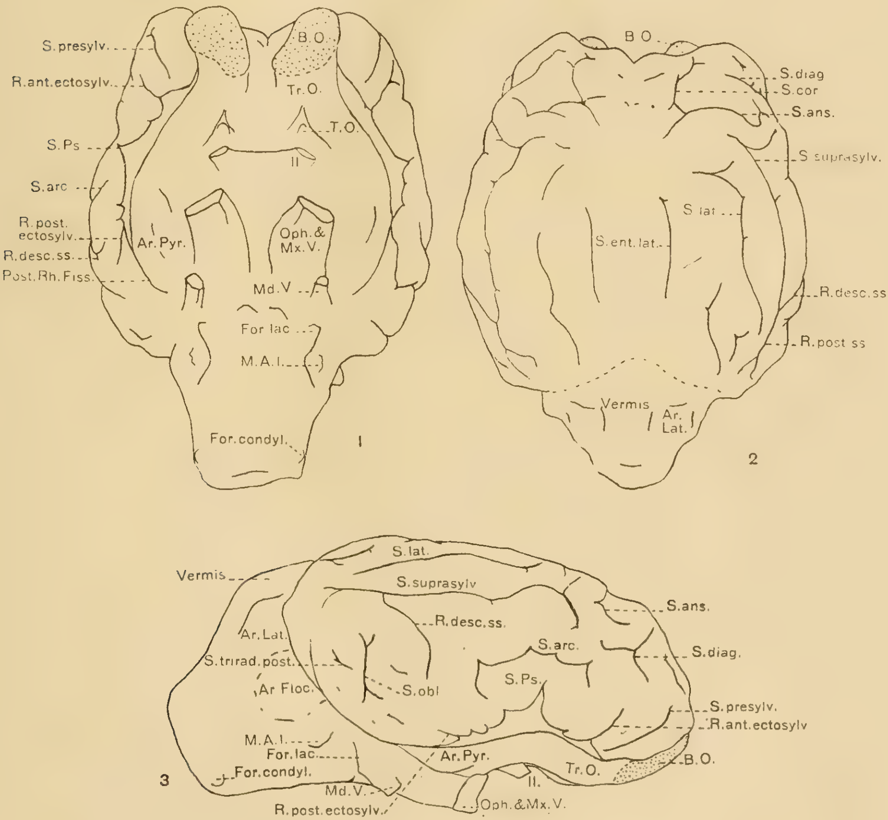
Brain stem, cerebellum and basis cranii. In a ventral view (figs. 1 and 17), the relation of the large sessile olfactory bulb (*B.O.*) to the tractus olfactorius (*Tr.O.*), is well shown. Between the diverging lateral and mesial olfactory tracts, which in the recent state occupy special bony grooves, a small prominence represents a depressed area in the skull floor for the lodgment

ABBREVIATIONS

Ar.Floc., floccular area
Ar.Lat., lateral area of interfloccular mass
Ar.Pyr., pyriform area
B.O., protuberance corresponding to fossa for lodgment of bulbus olfactorius
For. Condyl., protuberance corresponding to condylar foramen
For. Lac., irregularities marking site of foramen lacerum basis cranii
M.A.I., elevation indicating position of internal auditory meatus
Md. V., protuberance corresponding to foramen ovale transmitting the mandibular division of the trigeminal nerve
Mx. V., protuberance which apparently corresponds to the foramen rotundum for the passage of the maxillary division of the trigeminal
Oph. V., protuberance corresponding to foramen lacerum orbitale
Oph. & Mx. V., protuberance corresponding to skull groove lodging the first two divisions of the trigeminal nerve in their passage to a common exit at the foramen lacerum orbitale
Post. Rh. Fiss., posterior rhinal fissure
R. ant. ectosylv., ramus anterior ectosylvii
R. desc. ss., descending ramus of the sulcus suprasylvii
R. post. ectosylv., ramus posterior ectosylvii
R. post. ss., posterior ramus of the sulcus suprasylvii
S. ans., sulcus ansatus
S. arc., arcuate constellation
S. cor., coronal sulcus
S. diag., diagonal sulcus
S. ent. lat., entolateral sulcus
S. lat., lateral sulcus.
S. obl., oblique sulcus (of Holl)
S. presylv., presylvian sulcus
S. Ps., pseudosylvian fossa—processus acuminis
S. suprasylv., suprasylvian sulcus
S. trirad. post., triradiata posterior of Kappers
T.O., elevation corresponding to fossa lodging tuberculum olfactorium
Tr.O., ridge indicating skull groove for lodgment of the tractus olfactorius
Vermis, median area of interfloccular mass
II., tubercle corresponding to the position of the optic foramen

of the tuberculum olfactorium (*T.O.*). Behind this area a transverse groove caused by the posterior margin of the lesser sphenoidal wing marks the caudal limit of the anterior cranial fossa. The position of the optic foramina (*II.*) is indicated on each side of the cast by two dorso-ventrally compressed prominences, behind the trigonum olfactorium.

In the giraffe, as in the sheep and cow, the foramen lacerum orbitale and foramen rotundum form one large opening into



Figs. 1, 2 and 3 Outline drawings of endocranial cast of Giraffa camelopardalis, ventral, dorsal and right lateral views respectively. For lettering see list of abbreviations page 332. For the photographs from which these outlines were taken, see figures 17 to 19. About ½ natural size.

which pass the ophthalmic and maxillary divisions of the fifth nerve together with the oculomotor, trochlear and abducent nerves. The prominence labeled *Oph. & Mx.V* represents a deep skull groove, the floor of which is occupied in the recent state from the medial to the lateral side respectively, by the ophthalmic and maxillary divisions of the trigeminus. The rostral limit of this prominence corresponds to the position of the anterior lacerated foramen. The site of the foramen ovale transmitting the mandibular division of the trigeminus and the slight groove occupied by this root, is indicated in the figures by the legend, *Md.V*. From the base of this "mandibular" elevation a ridge is evident in figures 3 and 19, passing dorso-caudally, which represents a skull groove along the attached border of the tentorium. This groove leads into the parieto-temporal canal (meatus temporalis) and in the recent state is occupied by the vena cerebralis dorsalis, which is in turn continuous with the transverse sinus.

The internal auditory meatus for the passage of nerves VII and VIII is indicated by a circumscribed elevation capped by two bosses and situated about 10 mm. behind the base of the tentorial ridge. The VII and VIII eminence is placed in the middle of a somewhat depressed area which is moulded by the periotic bone. Inferiorly, this area terminates at the foramen lacerum basis cranii. Through this foramen in the recent state pass the internal carotid artery, the middle meningeal artery, the IX, X and XI nerves and the inferior cerebral vein. The position occupied by this foramen is indicated in the cast by the irregular ridges on each side of the basi-occipital or pontine region.

No indication as to the relative development of the pons and corpus trapezoides can be obtained from the cast. These structures are apparently separated from the floor of the bony cranium as in the cow, by a bridge of dura beneath which is lodged the plexus of the basilar sinus.

The position of the condylar foramen is evidenced by a slight elevation on the lateral, caudo-ventral surface of the cast.

This cast gives but little information as to the morphology of the cerebellum save to indicate the presence of cake-like floc-

cular lobes common in ungulates. The large interfloccular mass exposed between the caudally diverging cerebral hemispheres shows no evidence of division into medial and lateral areas.

Cerebral hemispheres. Upon the convex cerebral surface of the cast, the marks left by the cerebral ridges and digital impressions are so distinct, that the convolutional pattern may be interpreted clearly.

Dorsally (figs. 2 and 18) the relation of the lateral sulci to the suprasylivian arc is well shown. The coronal is caudally connected with the ansate sulcus, a common ungulate condition. This ansate sulcus is in no way to be compared with the somewhat similarly placed cruciate sulcus peculiar to carnivores.

The posterior rhinal fissure (figs. 1 and 3) limiting the pyriform area laterally, is well marked. Rostrally the anterior rhinal fissure is not so clearly indicated but may be made out as the ventral limit of a depressed area from whose dorsal boundary the ramus anterior ectosylvii emerges.

The presylvian sulcus, rostral to the ramus anterior ectosylvii may readily be identified but its continuity with the anterior rhinal fissure is not evident.

In my preliminary report (l. c.) I used Campbell's term "orbital sulcus" together with the term "paraorbital sulcus" to designate the "presylvian sulcus" and the "ramus anterior ectosylvii" respectively. The latter terms are more desirable, as both Kappers and Elliot Smith have shown that the so-called "orbital sulcus" of carnivores and ungulates is not in any way homologous to the sulcus bearing this name in primates. Furthermore Kappers has pointed out (21, p. 348) that the sulcus termed presylvian nearly always represents the caudal boundary of the area granularis frontalis and forms a line of demarcation between this area and the area giganto-pyramidalis or agranularis frontalis. If the term 'orbital sulcus' be discarded, it is obvious that the term 'paraorbital' has also lost its original descriptive significance, while the term 'ramus anterior ectosylvii' indicates at once the true relations of this sulcus.

The diagonal sulcus which is well marked on both sides shows no connection with the suprasylvian.

The whole course of the suprasylvian sulcus may be seen in a lateral view of the cast. In addition to the posterior horizontal limb common in ungulates, a long descending ramus of the suprasylvian sulcus is to be noted. This sulcus is probably not homologous with the postsylvian sulcus of carnivors, in which forms this sulcus is only separated from the lateral group of sulci by a comparatively small area.

The area ventral to the horizontal limb of the suprasylvian sulcus in the giraffe, as in the other ungulates, is of considerable extent, and is marked by two fairly constant sulci; the oblique sulcus of Holl and the constellation termed by Kappers the triradiata posterior (l.c., p. 309).

The pseudosylvian fossa is clearly indicated by a Λ-shaped, depressed area, the apical prolongation of which has been termed the processus acuminis. The caudal operculated lip of this fossa is notched by two or three slight compensating sulci and terminates in a well marked ramus posterior ectosylvii.

Between the processus acuminis of the pseudosylvian fossa and the suprasylvian sulcus, a well marked arcuate fissure is situated. This constellation is present on both sides of the cast and is indeed one of the characteristic features of the giraffe brain. It will subsequently be shown that this arcuate constellation is of distinct diagnostic importance when present together with the form of ramus descendens suprasylvii here described.

(b) *Ocapia johnstoni (figures 4 to 6 and 20 to 22)*

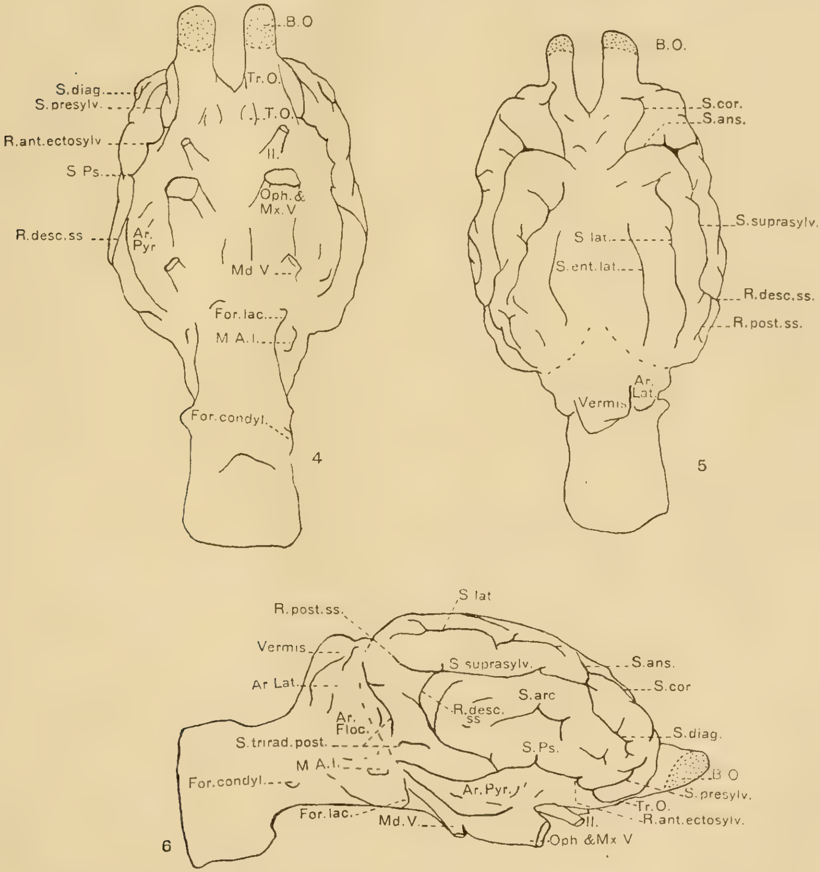
This member of the family Giraffidae was first discovered in the Belgian Congo in 1899. No material other than the skin and skeleton has as yet been available for scientific study. The facts relating to the discovery of this animal, together with notes upon its mode of life and detailed descriptions of its skeletal parts, may be had in the memoirs of Ray Lankester and Fraipont (l.c.).

In my preliminary report (l.c.) this animal was referred to as a 'hornless' form, and indeed the description in Beddard's text

(2, p. 305) states that 'there are no external horns.' This however is quite incorrect, for paired horns are present in the male though only represented by hair tufts in the female (18).

The volume of the endocranial cast is 450 cc.

As in the giraffe the greatest transverse diameter of the cast is in the parietal region, where it measures 100 mm. across. From the pontine surface to the highest point over the vermis the cast



Figs. 4, 5 and 6 Outline drawings of endocranial cast of Ocapia johnstoni, ventral, dorsal and right lateral views respectively. Abbreviations, see page 332. For photographs from which the outlines were taken, see figures 20 to 22. About ½ natural size.

measures 67 mm., which is but little less than the corresponding distance in the giraffe. From the frontal to the occipital pole of the cerebrum, the maximum length is 106 mm. The greatest interfloccular diameter is 55 mm.

Brain stem, cerebellum and basis cranii. The appearance of the cerebellar portion of the cast is of interest for, in contrast to the giraffe, its configuration is such as to yield some accurate information concerning the morphology of the interfloccular mass.

The two endocranial casts of this animal in my possession differ from each another considerably in the clearness with which the so-called vermis area is demarcated. Thus there is an individual variation in this region in the okapi. This, however, may be accounted for readily when the condition which obtains in this region of the skull among other ungulates is considered.

Le Double (25, p. 45) has pointed out that the inner surface of the skull in mammals in general is often moulded in its caudal part by the cerebellum to form three fossae: a median one for the lodgement of the median lobe ('fossette cerebelleuse moyenne"), and two lateral ones for the lateral cerebellar lobes. This median fossa is present in many ungulates. In these forms this author further notes (p. 49) that caudally the falx cerebri may ossify at its junction with the tentorium and give rise to a projection, the inferior surface of which is concave and continuous with the median cerebellar fossa. This projection overlaps the vermis to such an extent among the Equidae that it has been described by Albrecht (1) as the 'operculum of the vermis.'

Ossification of the tentorium, though common in adult Carnivora, is rare in ungulates, especially in artiodactyles. In the latter group no indication of Albrecht's operculum was observed in the skulls collected in the anatomical museum of this department except among the Cervidae, in which it was only indicated in the skulls of old animals (Cervus canadensis).

From this it is reasonable to infer that the difference in the appearance of the vermis region in the two okapi casts in my possession is one due to age.

The prominent asymmetrical boss formed in the mesial plane by the median lobe of the interfloccular mass is distinctly outlined and is separated by a well marked furrow from the less prominent lateral areas of this mass. Rostrally the median protuberance ends abruptly in a depression occupied in the recent state by the junction of the falx cerebri and the tentorium cerebelli. The lateral cerebellar swellings apparently correspond to those portions described by Elliot Smith (10) as Area B of the interfloccular mass (=Crus I of Bolk, 4). These lateral areas are placed dorso-caudal to the floccular region, from which they are only separated by an indistinct groove. On the whole it may be said that, in its general morphology, the cerebellar portion of this cast recalls the condition obtaining among the Cervidae.

Unlike the condition found in the giraffe, the olfactory bulbs in okapi are pedunculated and project a considerable distance beyond the frontal poles of the cerebrum. The fossae lodging the olfactory tracts are well developed.

It should be noted here that the asymmetry of the portion of the cast representing the olfactory bulbs and tracts and optic nerves is due to the defective restoration of these parts after they had been damaged on the left side.

As the remaining structures represented in the basal portion of the cast differ in no important detail in their general relations from those already described in the giraffe, further description of this region may be dispensed with.

Cerebral hemispheres. The arrangement of the sulci appearing upon the dorso-lateral surface of this cast gives evidence of a close relationship between the okapi and the giraffe. The arcuate constellation and the arrangement of the lateral group of sulci in the okapi are essentially similar in their relations to the corresponding furrows already noted in the giraffe. There are, however, not a few significant differences, to which attention will be drawn in the following description.

Dorsally (figs. 5 and 21) the relations of the lateral sulci to the coronal and suprasylvian are evident and present no unusual feature. However, the changed relations of the coronal, ansate

and suprasylvian sulci, together with the diagonal, are worthy of note. In the okapi, as is usually the case in the Cervidae and often in other ungulates, the ansate sulcus joins the coronal to the suprasylvian.

The suprasylvian is also continuous with the diagonal on the right side (fig. 6), though this is not the case on the left.

The continuity of the suprasylvian and the diagonal sulci is a common phenomenon among ungulates, appearing in both the Perisodactyla and Artiodactyla (figs. 10 to 16) and also among carnivors (11). This is regarded by Kappers as evidence that the diagonal sulcus is originally an anterior branch of the suprasylvian.

Thus the continuity of the suprasylvian and diagonal, which occurs on the right side, and the junction of the coronal and suprasylvian by the ansate, which occurs on both sides, represent, in the okapi, generalized ungulate characteristics which have been retained.

Laterally, the posterior rhinal fissure and the pyriform area lying below it may be clearly seen, but the anterior rhinal fissure cannot be definitely distinguished.

The pseudosylvian fossa is represented on the surface by a short vertical fissure and, as the frontal operculum is well developed, only a very small part of the anterior ectosylvian sulcus is visible.

The presylvian sulcus is large and extends frontad till it almost reaches the coronal, from which it is only separated by a narrow space.

The broad area between the short processus acuminis of the pseudosylvian fossa and the quite dorsally placed suprasylvian sulcus, is marked by a well developed arcuate constellation.

The descending ramus of the suprasylvian sulcus is well developed and differs from the sulcus bearing this name in the giraffe by being more caudally placed and by cutting the rhinal fissure. This communication with the rhinal fissure is apparently brought about by a junction of the descending ramus with the upturned ramus posterior ectosylvii, behind the caudal pseudosylvian operculum.

In the Cervidae and in other forms where the descending ramus of the suprasylvian is usually small, the oblique sulcus is large, and passes forward into the region which is occupied in the giraffe by the large descending ramus suprasylvii (figs. 10 and 12). Also in Cervidae, this oblique sulcus often cuts the posterior rhinal fissure, either independently or by joining the ramus posterior ectosylvii.

I have already (3) mentioned the possibility of the oblique sulcus in Cervidae (fissura postica of Krueg, fissura suprasylvia posterior of Flatau and Jacobson) being the homologue of the prolonged descending ramus of the suprasylvian in okapi. I am, however, inclined to modify this view somewhat on further study of the relations of the sulci in this region.

In the giraffe (fig. 3) the descending ramus of the suprasylvian, the oblique and the ramus posterior ectosylvii, are each to be distinguished as separate sulci. In the okapi, however (fig. 6), the sulcus termed ramus descendens suprasylvii is much more caudally placed and cuts the rhinal fissure (see also Samotherium, fig. 9). Thus, the arrangement of this constellation in the okapi is such as to suggest at least the possibility of its representing, not the oblique sulcus only, but rather a complex of three sulci, viz., the ramus descendens suprasylvii, the oblique and the caudal end of the ramus posterior ectosylvii.

The possibility of this is increased when it is remembered that such combinations of sulci are not rare, and that in this same cast other examples of such a phenomenon have been noted (corono-ansate-suprasylvian and also suprasylvian-diagonal).

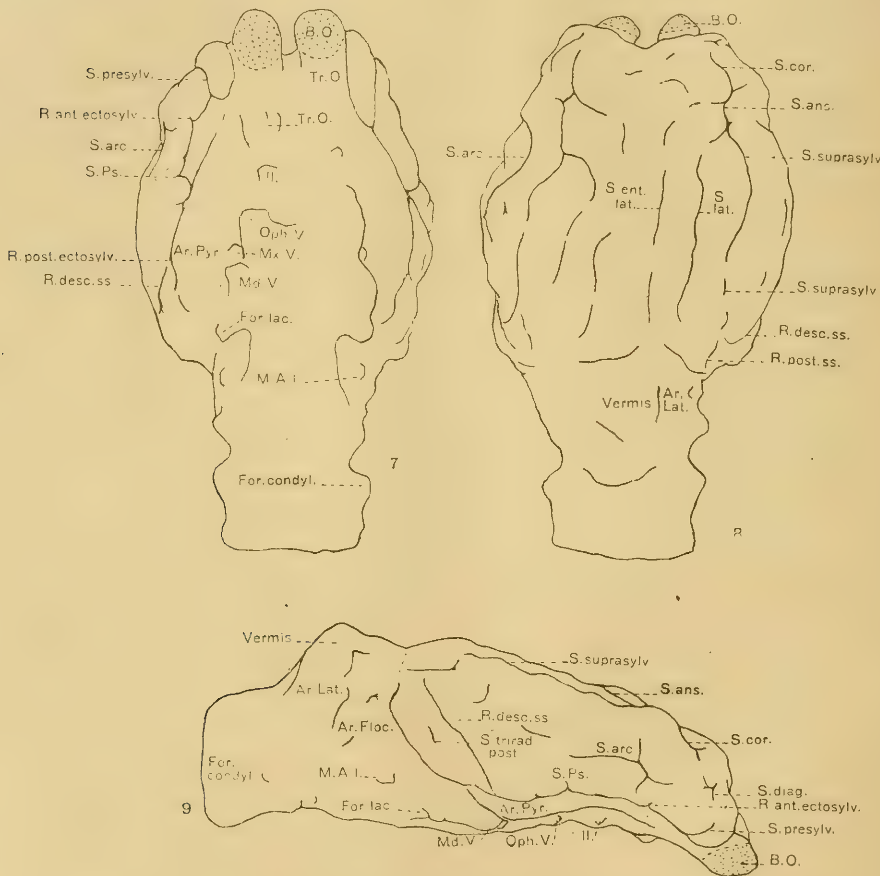
The irregular sulci marking the caudo-lateral surface of the cast are thus to be considered as representing the triradiata posterior of Kappers.

(c) *Samotherium* (*figures 7 to 9 and 23 to 25*)

This primitive ruminant, resembling the modern okapi, was discovered in upper Miocene deposits in the island of Samos (Forsyth Major, 15, 16). Like the okapi, horns were present only in the male and were situated upon the frontal bones.

As the result of considerable compression of the skull during fossilization, the endocranial cast is quite asymmetrical, and much detail in the ventral area has been obscured. Notwithstanding this unfavorable condition, it is possible to trace the course of the principal sulci with comparative ease.

The volume of the cast is 425 cc., which is but little less than that of the okapi. Indeed, if due allowance be made for the



Figs. 7, 8 and 9 Outline drawings of endocranial cast of Samotherium, ventral, dorsal and right lateral views respectively. For abbreviations see page 332. For photographs from which the outlines were taken, see figures 23 to 25. About ½ natural size.

above mentioned distortion, the volume of this cast would at least equal if not exceed that of okapi.

On account of asymmetry the following measurements may be compared only approximately with the similar measurements recorded for the giraffe and okapi.

The greatest transverse diameter of the cerebral portion of the cast in 96 mm. From the pontine surface to the highest point over the vermis area the distance is 60 mm. From the frontal to the occipital pole of the cerebral portion, the maximum length is 110 mm. The greatest interfloccular diameter is 57 mm.

Brain stem, cerebellum and basis cranii. In its cerebellar portion this cast resembles that of okapi, and like the latter there is evidence here of ossification having occurred in the dura to some extent in the region of the junction of the falx and tentorium. The presence of a well marked "fossette cerebelleuse moyenne" is indicated by the prominence of the interfloccular mass in the median plane. There is but little trace of the definite furrows separating this median prominence from the lateral portions of the interfloccular mass so obvious in the okapi.

The olfactory bulbs are pedunculated as in the okapi, and project a considerable distance beyond the frontal pole of the cerebrum.

It has already been noted, that the configuration of the ventral area is altered to some extent, but most of the landmarks of this region may still be recognized.

In figures 7 and 23, the protuberance marking the site of the right optic foramen is quite evident. Caudad from this certain elevations indicate the position of the emerging divisions of the trigeminal nerve. Between the protuberances which correspond to the foramen lacerum orbitale and the foramen ovale respectively on the right side an irregular elevation occurs which suggests the presence of a foramen rotundum. Though not so evident on the left, this possibility at least may not be excluded, from an examination of the cast alone. The presence of two separate foramina in the great wing of the sphenoid however, in any of the modern Ungulata vera, if it ever occur, must be a somewhat rare condition as may be judged from the following.

In Hyrax these three foramina are normally present. In Artiodactyla, so far as I am aware, the foramen rotundum is not present as a separate opening, while a distinct foramen ovale in these forms is characteristic. Among the modern Perissodactyla, a foramen rotundum occurs not infrequently in the Equidae, separated by a thin plate of bone from the foramen lacerum orbitale. In these forms, however, the foramen ovale is confluent with the foramen lacerum basis cranii (13), though the primitive stem perissodactyls were characterized by the presence of all three foramina (19, p. 390). The condition in the Indian elephant is similar to that in Artiodactyla in so far as the foramen ovale is discrete while the foramen rotundum and lacerum orbitale are confluent.

The remaining structures in this region correspond in general to the plan already described in the giraffe.

Cerebral hemispheres. A most interesting variation in the arrangement of the sulci in the dorsal view is seen in this case (figs. 8 and 24). While the entolateral sulcus occupies its usual position, the lateral sulcus becomes joined to the coronal as well as to the suprasylvian by the intermediation of the ansate sulcus.

The continuity of the suprasylvian and coronal sulci by way of the ansate is a common ungulate condition, while in Carnivora the lateral and coronal sulci are similarly associated. In the latter group of animals the junction of the coronal to the suprasylvian by the ansate is practically never present (21, footnote, p. 299).

The direct continuity of the lateral and coronal sulci is a very primitive feature in ungulates, which is recorded only in the hippopotamus (9, p. 321).

The condition obtaining in the present instance, however, in which these sulci are united by the ansate is not so rare an occurrence, though it represents a primitive arrangement in so far as it combines features common to both ungulates and carnivors.

The coronal sulcus, which is placed far forward, is comparatively small as in Hyrax. The diagonal sulcus is not continuous

with the suprasylvian on either side though it is almost so on the right.

The presylvian sulcus becomes evident a slight distance above the anterior rhinal fissure. Although it is placed far forward on the cerebrum, it is still separated from the coronal by a considerable interval on account of the shortness of the latter sulcus.

A sulcus recalling the carnivor "cruciatus," but not to be homologized as such, appears emerging from the sagittal furrow and probably represents the upturned termination of the splenial.

The anterior rhinal fissure is poorly marked as the ventral limit of a depressed area, whose dorsal border is formed by the frontal operculum of the pseudosylvian fossa. The ramus anterior ectosylvii is probably represented by the small notch in this operculum some distance behind the origin of the presylvian sulcus.

The pseudosylvian fossa is indicated on the right side by two or three small vertical notches, while on the left side the condition more nearly resembles that which has been described in the giraffe.

The suprasylvian sulcus is very dorsally placed and has a well marked, long descending ramus. The area between the pseudosylvian region and the suprasylvian sulcus is furrowed on both sides by a well developed arcuate constellation, which is in every respect similar to the sulcus bearing the same name in the giraffe and the okapi.

The relations of the caudally placed descending ramus of the suprasylvian in this form are such as to support the hypothesis put forward in the description of the okapi, viz: that this sulcus may represent a complex corresponding to the ramus posterior ectosylvii, the ramus descendens suprasylvii and the oblique sulcus. The small sulcus occupying the area caudal to the descending suprasylvian ramus of this form would thus represent the triradiata posterior of Kappers.

TYPES OF FISSURAL PATTERN ON THE LATERAL SURFACE OF THE CEREBRUM IN UNGULATES

Before discussing the possible significance of the data recorded in the preceding description, it will be well for the sake of comparison to consider briefly certain types of fissural pattern which obtain among ungulates other than the Giraffidae.

Only the sulci on the lateral surface of the cerebrum in forms belonging to the group Ungulata vera (Flower and Lydekker, 14) will be considered.

(1) Bos taurus (figure 10). The ectosylvian sulci are hidden in the ox for a large part of their extent by the frontal and caudal pseudosylvian opercula, which come together and form the large processus acuminis. The anterior and posterior rami of the ectosylvian may be seen as they diverge from the base of this sulcus. No doubt can remain as to the identity of these sulci since Holl's interpretation (vide infra, p. 352) has again been confirmed by the study of their ontogenetic development (Kappers, l. c., p. 289).

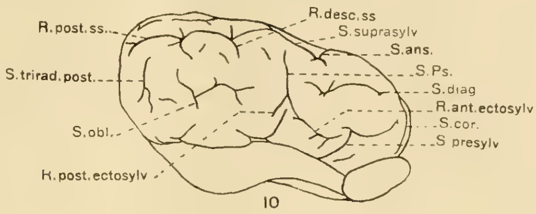
Below the diverging ectosylvian limbs is a somewhat depressed area limited ventrally by the rhinal fissure. From this fissure a Y-shaped notch extends upward as in the specimen figured by Elliot Smith (9, p. 343), and represents the homologue of the feline pseudosylvian sulcus. The presylvian arises from the anterior rhinal fissure. It is not connected with the ramus anterior ectosylvii as is the case in the specimen just cited, neither is it connected with the coronal as is often the case in Cervidae and other ungulates.

The diagonal is not connected with the suprasylvian, though the latter is linked to the coronal, as is frequently the case in the Bovidae and usually so in the Cervidae.

The suprasylvian sulcus is dorsally placed and gives off several secondary sulci. One of these, on account of its depth and its relation to the oblique, has been termed the ramus descendens suprasylvii in figure 10. A more characteristic arrangement obtains on the left side of this specimen, where the short descending ramus is closely related to a caudally placed upturned branch of the oblique. Behind the oblique sulcus an irregular

complex conforms to Kapper's description of the triradiata posterior (l. c., p. 309).

Posteriorly the suprasylvian sulcus ends in the characteristically ungulate fashion. There is no indication of an arcuate constellation as described in Giraffidae.



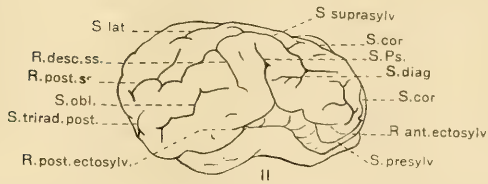


Fig. 10 Right lateral views of the cerebrum of a young specimen of Bos taurus. Abbreviations as before. $\times \frac{1}{2}$.

Fig. 11 Right lateral view of the cerebrum of Ovis aries (adult). Abbreviations as before. $\times \frac{1}{2}$.

(2) *Ovis aries* (*figure 11*). Compared with the ox, the posterior lip of the pseudosylvian fossa is in general somewhat further operculated in the sheep, so that all but the extreme caudal tip of the posterior ectosylvian sulcus remains hidden from the surface. Frontally also only a small part of the ramus anterior ectosylvii is exposed. The presylvian sulcus does not reach the rhinal fissure and is continuous frontally with the coronal.

The diagonal with its quite constant accessory sulcus (9, p. 340) is present on both sides. On the right the diagonalis proprius joins the suprasylvian.

The ansate joins the coronal sulcus but does not link the latter to the suprasylvian as in the ox. The long descending ramus of the latter sulcus is closely related to a simple linear oblique sulcus. The suprasylvian itself is prolonged caudad in

a characteristic ungulate fashion. There is no indication of an arcuate constellation between the long processus acuminis and the suprasylvian sulcus.

Variations in cortical pattern in the Bovidae

Although most members of this family conform more or less closely to one or other of the types of cortical pattern above exemplified, several exceptions are to be noted. Thus, the black-buck (Antilope cervicapra), the guib (Tragelaphus scriptus), the kudu (Strepsiceros kudu) and the eland (Taurotragus oryx) are each characterized by the shortness of the pseudosylvian processus acuminis and the development, between this sulcus and the dorsally placed suprasylvian, of a well marked compensating arcuate constellation (9, pp. 336 and 338).

(3) Cervus virginianus (figure 12). The operculation in the pseudosylvian region is rather more advanced in the deer than in the ox and sheep. The free extremities of the ectosylvian sulci are evident, however, as the ramus anterior and posterior respectively.

The presylvian is continuous with the coronal, while the latter sulcus is in turn joined to the suprasylvian by the arcuatus. The diagonal is independent of the suprasylvian.

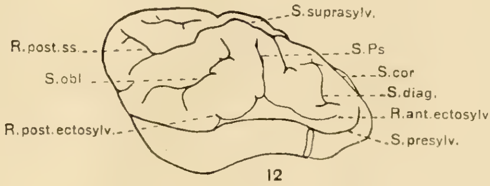
The descending ramus of the suprasylvian may be represented by the slight notch labelled as such in figure 12, but among the Cervidae this sulcus is either absent or but poorly developed, as frequently is the case in the Bovidae. The caudal bifurcation of the suprasylvian is well marked. The oblique sulcus is large and irregular in this form as in most of the Cervidae. It is possible that certain inconstant sulci behind the oblique may represent the triradiata posterior.

The long processus acuminis almost meets the suprasylvian. This is a characteristic phenomenon in Cervidae and precludes the formation of an arcuate constellation.

(4) Sus communis (figure 13). The operculation in the pseudosylvian area has progressed so far in Suidae that as a rule

only a small portion of the floor of this fossa remains exposed, as is shown in the specimen figured.

The large suprasylvian sulcus is fused anteriorly with the diagonal and is joined by an offshoot to the splenial sulcus as is usual in pigs. The latter sulcus however in this specimen is not joined to the coronal, though such a junction is usual in these forms.



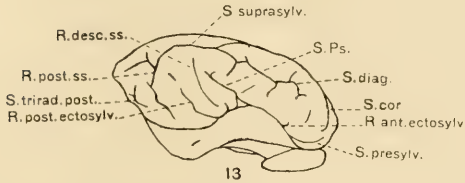


Fig. 12 Right lateral view of cerebrum of an adult specimen of Cervus virginianus. Abbreviations as before. $\times \frac{1}{2}$.

Fig. 13 Right lateral view of cerebrum of Sus communis (young adult). Abbreviations as before. $\times \frac{1}{2}$.

The presylvian sulcus is both well marked and separate from the coronal. On account of the extensive operculation already mentioned, the ramus anterior ectosylvii, which is small, appears to arise from the rhinal fissure.

Caudally one extremity of the bifurcated suprasylvian gives rise to a branch resembling the ramus descendens suprasylvii, but not to be homologized as such. Behind this sulcus lies the triradiata posterior.

The extensive upward prolongation of the ramus posterior ectosylvii is an unusual feature in the pig brain. In front of this is situated a linear sulcus which is curiously reminiscent of the sulcus E of Elliot Smith in the hippopotamus (9, p. 321) and it is possible that these sulci may both represent atypically

developed descending rami of the suprasylvian. There is no indication of an arcuate constellation.

(5) *Procamelus occidentalis* (*figure 14*). This figure has been inserted in the present series for purposes of comparison with the modern camel. The endocranial cast of this form has been described by Cope, from whose drawing (7) the outline in question has been taken.

The processus acuminis of the pseudosylvian fossa is seen to be well developed and only separated from the suprasylvian sulcus by a small space. The groove labelled descending ramus of the suprasylvian in figure 14, has precisely similar relations to the pseudosylvian fossa and upturned ramus posterior ectosylvii as the sulcus bearing the same name in the pig.

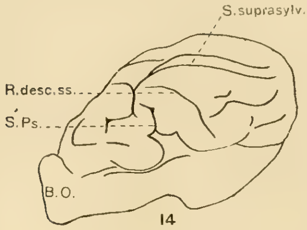
The long horizontal ramus of the suprasylvian, together with the lateral and entolateral sulci, is simple and linear, but without a re-examination of the cast their frontal relations are not clear.

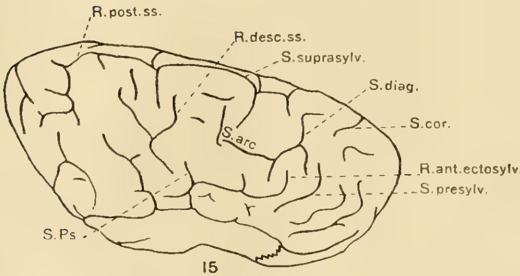
(6) *Camelus dromedarius* (*figure 15*). The above figure has been taken from Flatau and Jacobson's text (12, p. 432). Their drawing has been enlarged in the present instance until the fronto-occipital diameter was equal to this dimension in an adult skull of Camelus in the Reserve Anatomical Museum collection. In this way some idea of relative size can be gained.

In the camel the suprasylvian sulcus is quite dorsally placed, while the processus acuminis of the pseudosylvian is short. There is thus a broad area between these two sulci, which is marked by certain compensating furrows similar in nature to the arcuate constellation of Giraffidae. It is evident, however, from the arrangement of the sulci in the ancestral Procamelus (26, p. 300) that the arcuate group of sulci has been recently acquired in the camel.

The sulcus which I have labelled *R. desc. ss.* is termed by Flatau and Jacobson the 'fissura postica' or 'fissura suprasylvia posterior.'

(7) *Equus caballus* (*figure 16*). Among Perissodactyla in general, the presence of an arcuate constellation similar to that described in the Giraffidae, is a characteristic feature. In the





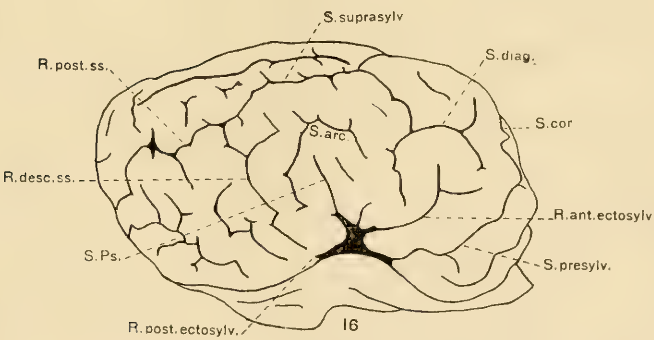


Fig. 14 Left lateral view of cerebral part of endocranial cast of Procamelus occidentalis. From a drawing of the cast described by Cope (7, plate 1, fig. 1, p. 36). Lettering as before. $\times \frac{1}{2}$.

Fig. 15 Right lateral view of cerebrum of Camelus dromedarius. (Modified from Flatau and Jacobson after Krueg (12). Abbreviations as before. About $\frac{1}{2}$ natural size.

Fig. 16 Right lateral view of cerebrum of Equus caballus (adult). Abbreviations as before. $\times \frac{1}{2}$.

horse this constellation is so constant and well marked that it has frequently been wrongly described as the ectosylvian sulcus.

The suprasylvian, coronal and presylvian sulci in the horse are usually in continuity as in this specimen, a condition which begins early in foetal life (5). The presylvian area in the horse is marked by an irregular sulcus, which is quite constantly present and has been termed the intraorbital sulcus (5) and (21, p. 293).

Reference to figure 16 renders further description of the specimen unnecessary in the present connection.

DISCUSSION

Arcuate constellation

The first point which requires consideration is the relation of the furrow which has been described in the foregoing account as the 'arcuate constellation,' to the ectosylvian arc.

Several authors, among whom may be mentioned Flatau and Jacobson (12), Sisson (27) and Bradley (5), have noted this sulcus in such forms as it occurs and have termed it the ectosylvian. It may be added that this sulcus is figured by Ellenberger and Baum (8, p. 779) and by Chauveau (6, p. 787) in the horse, but in neither case has it been given a name.

The error in using the term 'ectosylvian' as applied to this 'arcuate constellation' becomes apparent, however, when the following facts are considered.

Holl (20), Elliot Smith (9, p. 309 and elsewhere) and Kappers (l.c., supra), have already demonstrated that the pseudosylvian sulcus in ungulates is not at all homologous to the sulcus bearing the same name in carnivors. In the former group this sulcus is the result of either the partial or the complete submergence of the first arcuate or ectosylvian gyrus. The ectosylvian sulci are thus incorporated in the formation of the ungulate pseudosylvian sulcus, and depending upon the degree of operculation, are more or less hidden for a considerable part of their extent (figs. 10 to 13).

Anteriorly, however, the frontal extremity of the ectosylvian sulcus usually forms the well marked fissure termed the ramus

anterior ectosylvii. If, however, the frontal operculum of the pseudosylvian fossa be well developed, this sulcus may appear to take its origin from the anterior rhinal fissure (compare figs. 10 and 13).

In many cases also the posterior extremity of the ectosylvian sulcus appears on the surface as the ramus posterior ectosylvii.

It is obvious therefore that this arcuate constellation present in certain ungulates between the processus acuminis of the pseudosylvian fossa and the suprasylvian sulcus, does not in any way represent the homologue of the similarly placed ectosylvian arch of Canidae. It is indeed peculiar to certain ungulates, and has no homologue among carnivors.

It is evident that the arcuate constellation is not confined in its occurrence to the Giraffidae. Indeed it becomes increasingly manifest that the formation of this arched furrow, or series of furrows, is dependent upon the inter-relationship of the pseudosylvian acuminis and the suprasylvian sulcus. In the Perissodactyla, and equally in the Artiodactyla, whenever the acuminis is short and separated from the dorsally placed suprasylvian by a considerable interval, there appears quite constantly this additional arched fold, compensatory in nature, about the pseudosylvian region.

In all modern Perissodactyla the processus acuminis is usually separated from the suprasylvian sulcus by a broad area, and in this group the appearance of an arcuate constellation is a constant phenomenon.

In the Artiodactyla the requisite conditions for the occurrence of this constellation have been present among the Giraffidae since Miocene times. In the Camelidae on the other hand, these relations are of modern acquisition.

The ancestral conditions among the Perissodactyla and in the Artiodactyla other than the Giraffidae and Camelidae, have not as yet been examined.

Since a typical arcuate constellation has been independently aquired late in phylogeny among the Camelidae, it becomes evident that the mere presence of a well developed arcuate constellation in both the Equidae and the Giraffidae is in no way

indicative of a close relationship between the two groups. This would appear to be but another example of resemblance due to convergent or analogous evolution (vide Gregory, 19, p. 400).

Distinctive characters of convolutional pattern in Giraffidae

The chief peculiarities of the convolutional pattern in the Giraffidae, as evidenced by the material at my disposal, may be enumerated as follows: (a) a well marked and caudally situated ramus descendens suprasylvii; (b) a dorsally placed suprasylvian sulcus separated from the pseudosylvian acuminis by a broad area in which is developed a very evident arcuate constellation; (c) a small presylvian area (rostral to presylvian sulcus).

TABLE 1

	(1) R. DESCENDENS SUPRASYLVII	(2) ARCUATE CONSTELLATION	(3) PRESYLVIAN AREA
Giraffidae	Well marked and caudally placed	Present	Small—no sulcus intraorbitalis
Cervidae		Absent	
Antilocapridae		Absent	
Bovidae		Absent	
Bovidae* (exceptions)	Variable and when present, not so caudally placed		Usually larger than in Giraffidae
Tragulidae		Absent	
Camelidae	Usually separated from suprasylvian and not so caudally placed		Large—sulcus intraorbitalis well developed
Hippopotamidae		Absent	
Suidae		Absent	
Equidae	Not caudally placed		Large—sulcus intraorbitalis well developed
Tapiridae	Frequently separate from suprasylvian		Similar to Equidae
Rhinocerotidae	Similar to Equidae		Similar to Equidae

* Vide supra, page 348.

So far as the brain is concerned, the foregoing characters, when present in combination with one another, appear to be distinctive of the Giraffidae among the various groups comprising the modern Ungulata vera, as may be seen from the accompanying brief comparative summary (vide table 1).

CONCLUSION

From a comparison of the endocranial casts of the Giraffidae considered in this paper it becomes evident that among these the cast of Samotherium shows undoubtedly the most primitive arrangement of sulci, presenting as it does certain features common both to the Carnivora and to the Ungulata. In other respects however, this brain shows evidence of considerable specialization. Thus it will be noted that this early form is already possessed of certain brain characters which still serve to distinguish the Giraffidae among modern ungulates.

This early specialization of the convolutional pattern in the Giraffidae presents a marked contrast to the condition obtaining in the Camelidae of the same epoch (upper Miocene) as evidenced by the endocranial cast of the American form Procamelus occidentalis. The latter cast shows but little if any indication of a distinctive cameloid arrangement of sulci (vide p. 351).

In both Ocapia and Samotherium the brain presents certain generalized characters in the arrangement of the cortical pattern which are common and peculiar to the Ungulata, such for example as the relations of the corono-ansate-suprasylvian complex. In this category also I am inclined to consider the sulcus described in Ocapia and Samotherium as the ramus descendens suprasylvii, in so far as it may represent in these forms three sulci which are no longer continuous in the giraffe (viz., the caudal part of the ramus ectosylvii posterior, the ramus descendens suprasylvii and the sulcus obliquus).

In the giraffe there appear certain specialized characters which serve to distinguish this form from both Ocapia and Samotherium; such for example as the complete separation of the corono-

ansate from the suprasylvian sulcus and also the presence of the three discrete sulci mentioned in the preceding paragraph which appear to be merged in a single complex in Ocapia and Samotherium.

The curious superficial resemblance of the giraffe brain to that of the horse must be considered as the result of analogous or convergent evolution. Further consideration of this interesting condition however is left to a later date, when it is hoped to extend these observations by the examination of an extensive series of endocranial casts from allied forms, both recent and extinct.

Finally, the present study emphasizes once more the value of endocranial configuration as an index to the morphology of the brain, the taxonomic importance of which has long been recognized (11).

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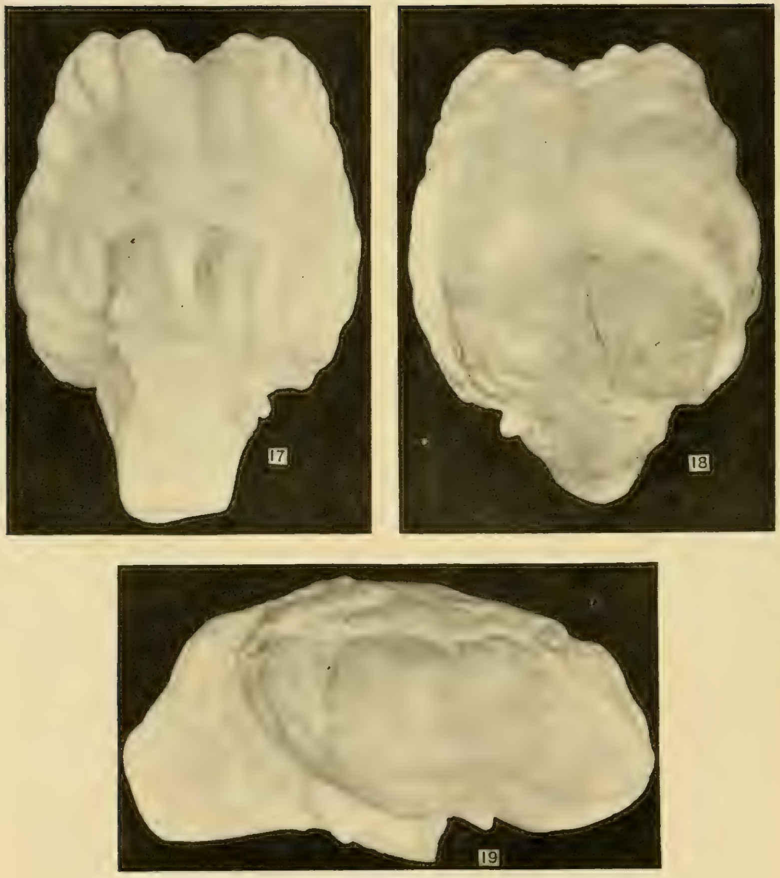
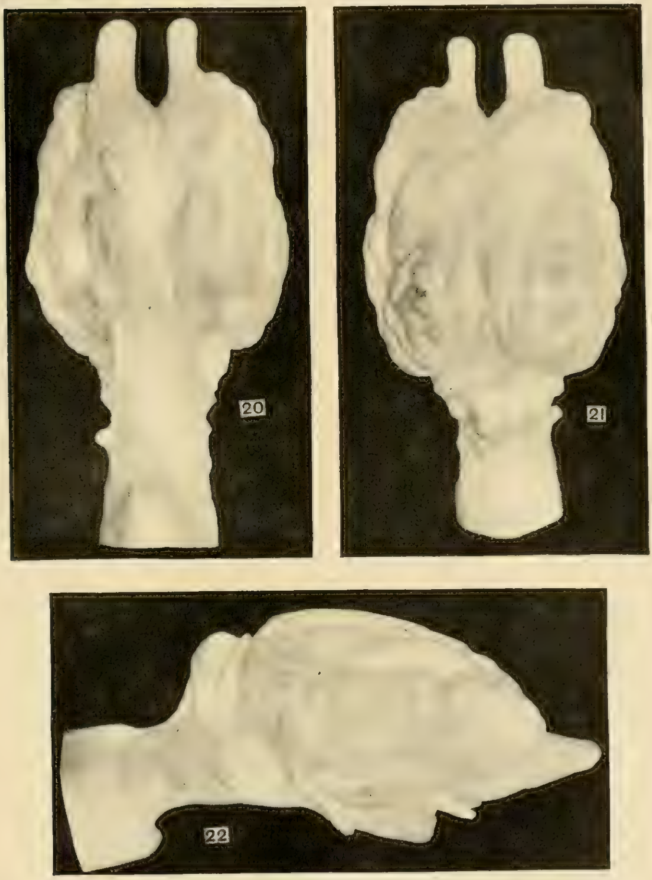
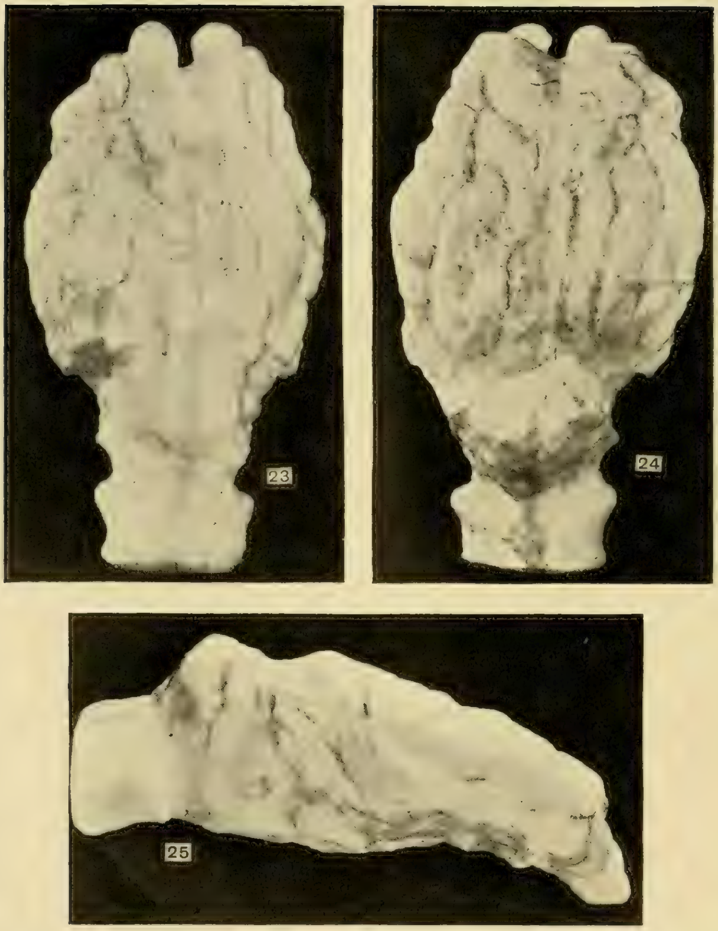


Figs. 17, 18, 19 Photographs of endocranial cast of Giraffa camelopardalis, ventral, dorsal and right lateral views respectively. About ½ natural size.



Figs. 20, 21, 22 Photographs of endocranial case of Ocapia johnstoni, ventral, dorsal and right lateral views respectively, About ½ natural size.



Figs. 23, 24, 25 Photographs of endocranial cast of Samotherium, ventral, dorsal and right lateral views respectively. About $\frac{1}{2}$ natural size.

A CASE OF UNILATERAL CEREBELLAR AGENESIA

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TWENTY FIGURES

The brain in this case came into the hands of the writer in the course of collecting some brains for anatomical purposes. The clinical symptoms were not thoroughly studied and recorded, but the following details were procured some time after from the physician in charge in reply to a letter of inquiry by Prof. M. Allen Starr.

The child, a girl, was 3 years, 4 months, 16 days old. She was a small child, her head was small and she was very weak and unsteady in all her movements. She sat up all day in a high-backed chair. She could walk, but with a very uncertain gait, staggering to one side (which side not noted) and with a tendency to hold fast to chairs, etc., in getting about. She was unsteady in grasping a proffered object. She could move her head but the movements were slow. No paralysis was noted. She had marked bilateral nystagmus, exact type not noted. Whether she was deaf in either ear was not noted. She was very weak mentally, appeared very dull, took little interest in toys, etc. She talked poorly and indistinctly, with scarcely any formed sentences. No convulsions nor spasms were noted, nor vomiting except during her last illness. It was not possible to be sure whether she had headache, but for many weeks after admission to the institution of which she was an inmate she cried almost constantly and rolled her head from side to side. After this crying ceased she almost continuously during the day hummed, without words, a few tunes, one popular air of the time especially. This humming was so marked, so continuous during the day, as to be a 'ward joke'—and accompanying the music, a never ceasing rotation of the head from side to side, usually in time with the music, and eventually resulting in depriving the back of the head of hair. Death was due to measles and broncho-pneumonia.

The brain was fixed *in situ* by intravascular injection with formalin not long after death and was consequently n excellent condition both as regards histological fixation and freedom from

artificial deformation when removed. The following observations were made upon the external characteristics of the brain, most of which were published in a preliminary communication (Jour. Comp. Neur., vol. 11, no. 1) and are repeated here, with slight changes, for purposes of completeness.

The most striking feature of the brain, externally, was the almost complete absence of the left hemisphere of the cerebellum. With the exception noted below, no part of the cerebellum extended more than 2 or 2.5 cm. to the left of the median line. This was true except a small lobe, apparently in part representing the flocculus, which protruded some 4 cm. to the left of the median line, dorsal to the VIII, IX and X nerves (figs. 1, 2, 3 and 4). Some preliminary transverse cuts showed apparently an absence of the left nucleus dentatus. (Subsequent sections revealed a minute left nucleus dentatus.) The inferior and superior vermis was apparently in part at least present. It was difficult to tell what the left lateral part represented morphologically, whether part of the vermis or part of the hemisphere (figs. 2, 3 and 4). All of the external surface of the cerebellum appeared normal, but portions of the left lateral surface revealed in sections an irregular, disordered histological arrangement (p. 369).

The cause of the agenesia was not clear, it was possibly due to some old, prenatal, cyst which occupied the space which should have been filled by the left cerebellar hemisphere.

On the ventral aspect (figs. 1 and 2), the right olivary body was apparently entirely absent (cuts made through the medulla have shown that a moiety of it was present); the left olivary body was normal. The cranial nerves were apparently normal.

The pons was highly asymmetrical. The transverse fibers, as viewed externally, were normal on the right side but enormously reduced on the left side laterally to the protuberance of the pons caused by the longitudinal tracts and nuclei within (i.e. the left middle cerebellar peduncle), so much reduced that the V and VII nerves, instead of being separated by the usual mass of transverse pontile fibers, issued from the pons in immediate contiguity to each other. On the other hand, the pons *pro-*

truded much more on the left side, indicating a greater development of the nuclei pontis and longitudinal pontile fibers on that side (fig. 1). The left crusta was wider than the right.

A dorsal view of the brain stem, the cerebellum removed (fig. 5) showed the following: The median line showed here, as well as on the ventral view, a marked curvature with the convexity toward the left. This may have been due to the position in which the brain, with the cord attached, rested in the jar of formalin but the fact that the brain was well hardened *in situ* by injections of formalin rendered this less probable.

The left clava was more elongated, extending further cephalad than the right and was also narrower. The same was true of the left cuneus. In the floor of the fourth ventricle, the left ala cinerea extended much (nearly 2 mm.) further cephalad than that on the right. The two trigona hypoglossi were nearly symmetrical; the left eminentia teres was further cephalad than the right. The left trigonum acustici was also further cephalad than the right and appeared to be somewhat less prominent (fig. 5). It would seem that this asymmetry of these structures is attributable in part or in whole to the unequal pressure exerted upon the medulla during its growth by the unequally developed halves of the cerebellum. The fact that the left clava and cuneus is longer and narrower than the right produces an inequality in size of these structures in transverse sections which might be wrongly attributed to an inequality of development, but is really only a difference of shape.

The left corpus restiforme was much smaller than the right. The funiculus separans (Retzius) and area plumiformis (Retzius) were present on each side. The striae acusticae were not visible. The sides and roof of the fourth ventricle exhibited asymmetrical markings.

The right superior peduncle was much larger than the left. The taeniae pontis were present on both sides but much more prominent on the left, the accessory bundle from the groove between the lingula and velum noted by Retzius (das Menschenhirn, p. 49) being observed.

The inferior colliculi were asymmetrical, the left being narrower, more prominent and protruding further caudad, its brachium appearing less prominent than that of the right.

The left superior colliculus appeared to be largely lacking. The same external causes which possibly operated to arrest the development of one side of the cerebellum might also have operated in this region.

The iter narrowed funnel-like to a point at the level of the inferior colliculi where it had the diameter of a mere pin-prick. The forebrain showed an internal hydrocephaly with dilatation of all parts of its ventricles.

The brain stem, with the cerebellum removed, was cut transversely into slices about 0.5 cm. thick. The pieces were mordanted in bichromate of copper 3 per cent for 7 or 8 days and imbedded in clove-oil celloidin. The sections were stained in haematoxylin (10 per cent solution of hematoxylin in absolute alcohol 1 vol. + water 9 vols.) about 12 hours at the temperature of the room. They were then rinsed in water, dipped in osmic acid about $\frac{1}{4}$ of 1 per cent for a fraction of a minute and decolorized by the Pal method.[1]

The greater part of the sections was prepared by one of the writer's students, C. E. Doran, who was to complete and publish the work. The unfortunate death of Mr. Doran just when he was beginning his study of the material caused the work to be laid aside.

There are some serious gaps in the series of preparations, involving the connections of the cerebellum, which was removed before sections were made, and also in the region of the superior colliculi and further cephalad. Because of these the case will not be made the basis of a more extended study and discussion and the present article will be limited to a bare description of the peculiarities observed. Reference should be made however to

[1] For further details concerning the use of copper bichromate and other experiments with the Weigert method, see the writer's article "Notes on the technique of Weigert's method for staining medullated nerve fibers." Journ. Comp. Neur., vol. 13, no. 4. Instead of using Pal's oxalic acid-potassium sulphite mixture after the permanganate, sulphurous acid diluted with about ten volumes of water will answer as well or even better.

the case reported by Edinger (Berliner Klinische Wochenscrift, Jahrgang 35, Nos. 4 and 5, 1898) which bears a remarkable resemblance to this. In Edinger's case, a man of 46, it was the right half of the cerebellum which was defective.

Sections through the cervical cord (fig. 6) do not reveal any very noticeable asymmetry. The right posterior horn is larger than the left but this is possibly due to the same causes which produced a narrower and longer clava and cuneus on the left (see p. 363). The left dorsal spino-cerebellar tract is, however, smaller than the right, being about 75 to 80 per cent of the size of the latter.

Sections through the bulb at the caudal extremity of the inferior olivary nucleus (fig. 7) show the following asymmetries. The right nucleus cuneatus and nucleus gracilis are larger than the left; the right external nucleus of the column of Burdach is present but not the left; external arcuate fibers are present on the right lateral periphery but not on the left; the left nucleus arcuatus and left medial accessory and principal inferior olivary nuclei are larger than the right. Of these asymmetries the asymmetry of the nuclei of the columns of Goll and Burdach is due to their longer and narrower shape on the left and may not indicate any true inequality in their development. The left external nucleus of the column of Burdach appears in sections further cephalad (fig. 8) and while it may be smaller in actual size than the right one this cannot be easily determined. External lateral arcuate fibers on the left appear in sections further cephalad and any true inequality is not very marked. Ventral external arcuate fibers are present here on both sides. It is not easy to ascertain slight inequalities in these on the two sides; but while those coursing around the pyramids are about equal at this level, further cephalad both those coursing around the pyramids and those running along the ventro-lateral periphery, outside the olive appear to be more numerous on the right. The left arcuate nucleus appears to be consistently larger than the right in sections through the lower olivary region but higher this nucleus disappears on the left and one appears on the right, but on the mesial aspect of the pyramid. If this latter be re-

garded as the equivalent of the more caudally located left arcuate nucleus, there may not be any marked inequality between the right and left nuclei. The right nucleus s near the pons, though, and may possibly be simply a part of the pons nucleus ("nucleus precursorius pontis"). The asymmetry in the inferior olivary nuclei might be due to obliquity of the section but subsequent sections (see below) reveal an enormous asymmetry in these nuclei involving both the principal and accessory nuclei.

Laterally and dorso-laterally to the left olivary nucleus and lying next the periphery are aberrant pyramidal fibers (figs. 8, 9, 10 and 11) which detach themselves from the left pyramid just cephalad of the olive (fig. 11) and rejoin the pyramid just caudad to the same. The bundle of fibers cut obliquely and lying near the periphery ventro-lateral to the left olivary nucleus in figure 7 is an aberrant bundle of this character which rejoins the pyramid a short distance below this level. Such aberrant fibers do not separate from the right pyramid but bundles can be seen (figs. 8 and 9) lying laterally to the atrophic olivary nucleus. The complete separation on the left is evidently due to the large left olivary nucleus and this difference is one of a number of peculiarities in the present case which illustrate the influence of mere spatial accommodation in determining the positions of various tracts and nuclei.

Sections through the lower and middle olivary levels of the bulb, and through the hypoglossal nucleus (fig. 8) display very strikingly the inequality in the development of the right and left inferior olivary nuclei. The principal right olivary nucleus is a U-shaped nucleus ranging from about one-third to one-fifth the area of the left nucleus. The accessory olivary nuclei show the same great reduction in size. Examination of the series of sections through the olives shows that the caudal part of the right principal olivary nucleus is less atrophied than the cephalic part. This is shown by the fact that it extends nearly as far caudad as the left and its caudal part is the largest part. Further cephalad it diminishes in size and ends some distance caudad of the cephalic end of the right nucleus. The right medial accessory olivary nucleus is about as well developed as the right

principal nucleus while the right dorsal accessory olivary nucleus is almost entirely absent, only the barest vestige being discernible in a few of the sections. The right olivary nuclei appear somewhat different microscopically, in the Weigert-Pal preparations, from the left. They contain fewer coarse fibers, apparently more fine fibers, especially at the periphery, and apparently fewer nerve-cells. They contain, however, nerve-cells of normal appearance. These appear to be very few in number in the cephalic, most reduced, part of the principal nucleus. A comparison of the transverse fibers of the two sides is interesting. On the right are seen dorsally the fibers passing principally from the nucleus cuneatus to the opposite fillet, ventrally are seen numerous fibers from the left side which pass through or dorsal to the right olivary nuclei and thence dorso-laterally, through or around the gelatinous substance of Rolando and spinal root of the trigeminus to the right restiform body. These latter, olivo-cerebellar, fibers are practically absent entirely on the left and the course of the fillet fibers is rendered especially clear. It will be noted that there are lateral external arcuate fibers to the restiform body on both sides and that the right restiform body is already decidedly larger than the left. Attention has already been called to the aberrant pyramidal fibers (p. 366).

The lateral reticular nuclei are present on both sides. Owing to their lack of clear outlines, it is not easy to detect any slight inequality but if there be such it is not very great.

In sections at the level of the emergence of the glosso-pharyngeus and cochlear portion of the acusticus (fig. 9), the great disparity in size between the left and right restiform bodies and the inequality of the olives are still more marked and are the most striking features. The left restiform body is, however, nearly three times the size of the left dorsal spino-cerebellar tract in the cervical cord. This accession of fibers would be from the external arcuate fibers and the small right olive. The great disparity in size between the two restiform bodies is obviously due entirely or almost entirely to the enormously greater number of olivo-cerebellar fibers received by the right restiform

body. These fibers are still seen in the section crossing from the left olivary nucleus, and their presence makes a striking contrast between the right side and the left where they are practically completely absent from the area between the left olive and the left restiform body. When it is considered that there is a moiety of left cerebellum present, it is evident that the olivo-cerebellar connection might, as far as conclusions can be drawn from this, be a completely crossed one and while there may be some uncrossed olivo-cerebellar fibers they must be relatively unimportant. It is evident also that the olives are connected at least as much with the cerebellar hemispheres as with the vermis, possibly more.

It will be noticed that the left descending vestibular root is smaller than the right. This is due partly or entirely to the fact that the section passes farther below the entrance of the left than the right vestibular nerve. The asymmetry of the two medial vestibular nuclei seen in the figure would be due to the same cause. Whether there is any difference in size between the two vestibular nerves could not be very well determined. It is seen that the medial longitudinal fasciculi are equal. It will also be noticed that the right medial fillet appears larger than the left.

A section through the entrance of the left cochlear nerve is shown in figure 10. The section also passes through the small left cerebellar hemisphere. In this section the left restiform body is seen at its maximum size. An interesting feature resulting from the lack of development of the left middle cerebellar peduncle is the partial exposure of the left trapezoid body. The trapezius fibers are seen issuing from the ventral cochlear nucleus, passing just caudad to the vestibular root and thence mesially near the periphery. Figure 11 shows a portion of the same, under a higher magnification, further cephalad. An aberrant pyramidal bundle (p. 366) is seen passing laterally to assume a position dorso-lateral to the olive farther caudad.

Figure 10 shows still more clearly the interesting but unexplained fact that the right medial fillet is larger than the left, the latter being about 80 per cent the size of the right. If it

be assumed that some of the fibers of the medial fillet terminate in the superior colliculus—which is disputed by some—the atrophy or agenesia of the latter might account for this. Imperfections in the series did not permit this point being fully investigated.

Sections further cephalad indicate that the fibers of the left juxta-restiform body, connecting the vestibular area with the vermis cerebelli are reduced in number, though present. Defects in the sections prevented their being followed into the cerebellum.

A section just caudal to the exit of the left trigeminus (fig. 12) shows the position and maximum size of the left, atrophic, nucleus dentatus. Dorsal to it is a rounded mass of abnormal cerebellar cortex (compare fig. 5, *1*).

Figure 12 also shows the abnormal features of the pons. On the left the pons consists almost entirely of gray, the pontile nuclei, through which the longitudinal bundles of the pyramid are proceeding. From these nuclei transverse pontile fibers pass across to the right and accumulate on the extreme right as the right brachium pontis or right middle cerebellar peduncle. On the other hand, the right pontile nuclei are almost entirely absent and the same is true of the left middle peduncle, there being only a light-staining mass containing scattered fibers. While it is obvious that this shows the ponto-cerebellar connection to be mainly a crossed one, the possibility of there being a small minority of uncrossed fibers cannot be logically excluded.

It will be noticed also (fig. 12) that the ventral part of the tegmentum, laterally to the left medial fillet, contains masses of gray not present here nor further cephalad on the right and not usually found so extensively here. Nerve cells of normal appearance are present in them. It is suggested that the left pontile nuclei are somewhat hypertrophic and have invaded the tegmentum. Among the ordinary transverse fibers decussating through the medial fillets are bundles of fibers resembling the transverse pontile fibers in stain. They are found in this and other sections of about this level on both sides. It is difficult to trace their origin and destination but they appear to arise

or end in either the pons or the masses of gray above mentioned. Some of them can be traced into the pons. Some of these bundles are shown in a higher magnification in figure 13. They would thus seem to be aberrant pontile fibers. Besides these bundles there are other bundles seen on the right side in the central gray which on the one hand pass dorsally along the side of the ventricle (fig. 12) and on the other hand, at a higher level (fig. 14), pass ventrally into the right reticular formation. Where this occurs there are streaks of gray, also containing nerve-cells of normal appearance, in the reticular formation (fig. 14) with which they appear to be connected. Some of these bundles, at least, pass into the pons laterally to the medial fillet. It hardly seems possible that any of these bundles could represent aberrant striae medullares and they must be looked upon as abnormal. Other similar peculiar bundles connected with the central gray at higher levels will be noted below.

No definite indications were noted of an asymmetry in the perpendicular pontile fibers nor of the various tegmental nuclei (nucleus centralis superior, etc.) except the nucleus ruber.

The left central tegmental tract is very well developed and conspicuous while the right one is completely or nearly completely absent.

Sections through the isthmus (figs. 15, 16 and 17) show strikingly the above inequalities in the pons and in the central tegmental tracts. The right superior cerebellar peduncle is fully or even over normal size while the left is represented by a few small bundles hardly apparent in the figures, but representing apparently dorsal, middle and ventral parts of the peduncle. It is interesting to note here again how these inequalities in large bundles of fibers entail asymmetrical arrangements of other structures themselves normal. In figure 15 the left lateral fillet has assumed its dorsal position along the side of the tegmentum while the right is still close to the pons. The asymmetry of the medial fillet is also largely due to the fact that the left fillet has passed further laterally than the right. While these appearances may be due partly to obliquity of the section, they must be regarded as largely due to the adjustment required

by the nearly complete absence of the left superior cerebellar peduncle and perhaps in some measure to the practical absence of the right central tegmental tract.

The left mesencephalic root of the trigeminus is only about half the size of the right. It is difficult to tell, on account of deficiencies in the series, whether this is connected with the defect of the left superior colliculus.

In figure 15 an interesting asymmetrical bundle is seen on the right issuing from the central gray and passing ventrally in the raphé. Its fibers could not be traced with certainty to the perpendicular pontile fibers but this connection seemed probable. From this bundle while in the central gray a small bundle passes laterally into the reticular formation. In figure 17 another bundle is seen on the left passing from central gray into reticular formation. It is connected with a snarl of fibers seen in the central gray, apparently an abnormal condensation or local increase in the plexus of medullated fibers normally found in the central gray. Another similar appearance is noted below (p. 372). A possible cause for these phenomena that suggests itself is that they are due to the irritative effects of an ependymitis at an early period of development. The other bundles in the central gray noted above are perhaps similar in character. Some of these bundles may be more an increase of fibers normally present than entirely new appearances. In this case they might throw some light on the rather obscure connections of the central gray.

In comparing the pons at various levels it will be noted that there is a steady increase in the longitudinal fibers in the left pons. At the lowest level of the pons the longitudinal fibers (here almost exclusively pyramidal fibers) are about equal on the two sides. At the upper levels of the pons the longitudinal fibers on the left are, as far as can be made out, about double those on the right. This discrepancy is not so apparent on casual inspection on account of the greater number of transverse pontile fibers on the right and the great number of middle peduncular fibers accumulated on the lateral border.

In the region of the inferior colliculus (fig. 18) the most striking feature is the great inequality in the fibers of the pes on the two sides. The sectional area of these fibers on the left is just about three times the area of those on the right. The fibers present on the left but not on the right are, of course, the pallio-pontile fibers which terminate in the pontile nuclei. The fibers of the right pes would be composed almost entirely of pyramidal fibers and as a matter of fact the area of the right pes is not far from that of one of the pyramids below the pons.

An interesting fact, very apparent in the sections, is that the substantia nigra varies *pari passu* with the pes. The disproportion between the right and left substantia nigra is nearly, though not quite as great as that between the right and left pes. This would seem to indicate a close connection, probably by collaterals, between the two. This connection, however, would not necessarily be only between the pallio-pontile and pyramidal fibers and the substantia nigra. At a higher level (fig. 19) the discrepancy in size between the right and left pes and between the right and left substantia nigra, especially the latter, is apparently much less. This would rather point to descending fibers which entirely end in the substantia nigra. The above-mentioned facts about the right pes, its diminution from subthalamic to prepontine region and its practical equality in size with the pyramid not only favor the pes containing, at the former level, fibers which terminate in the nigra but militate against descending fibers in the pes which originate in the nigra.

In figure 18 the decussation of the superior cerebellar peduncle is shown, or rather the crossing of the right peduncular fibers to the left side. The portion of the left peduncle here distinguishable is represented by a few uncrossed straggling fibers dorsal to the left central tegmental tract. The rest is crossing or has already crossed to the right.

Dorsal to the iter is seen another tangle of fibers in the central gray similar in character to that already noted.

The principal point to be noted in the sections at hand of higher levels is the absence, as far could be ascertained, of the right nucleus ruber. Owing to a serious gap in the series it could not

be ascertained whether it was completely absent or simply much reduced in size, but its absence contrasted with the large left nucleus is a striking feature in figures 19 and 20. Besides this and correlated changes in the field of Forel no other changes were noted at these higher levels.

CONCLUSIONS

1. The following structures were found to be markedly defective: The greater part of the left cerebellar hemisphere, possibly a part of the vermis and the left superior colliculus; the right inferior olivary nuclei, the right central tegmental tract and the left corpus restiforme; the left middle cerebellar peduncle, the right pons nuclei, the right pes and the right substantia nigra; the left nucleus dentatus, the left superior cerebellar peduncle and the right nucleus ruber. All of these findings are simply confirmatory, or illustrative, of the accepted views as to the cerebellar connections involved. It may be pointed out again that, while uncrossed olivo-cerebellar and ponto-cerebellar (from pontile nuclei) connections are not entirely excluded, they either do not exist or are relatively inconsiderable and that the great majority at least of the olivo-cerebellar fibers are distributed to the cerebellar hemispheres.

2. The following structures usually supposed to be connected with the cerebellum were found to be, as far as could be ascertained, either normal or possibly slightly defective: The dorsal and ventral spino-cerebellar tracts (the dorsal slightly defective on left), the arcuate nuclei (defective on right possibly), the ventral and ventro-lateral external arcuate fibers (slightly defective on left possibly), the lateral reticular nuclei, the external nuclei of the column of Burdach and other nuclei of Goll and Burdach, the juxta-restiform bodies (vestibulo-vermis connections, possibly somewhat defective on left); the perpendicular pons (ponto-tegmental) fibers and certain tegmental nuclei. If these structures are connected with the cerebellum, we would be obliged logically to assume either that each is connected equally with both hemispheres of the cerebellum or they are mainly connected with

the vermis. The latter conclusion is certainly true of some of these and may very well be true of all. If this be accepted, we have on the one hand the great afferent tegmento (?)-olivo-cerebellar and pallio-ponto-cerebellar paths principally to the cerebellar hemispheres which are affected greatly and on the other hand the afferent paths from the periphery via spino-cerebellar paths (whether interrupted in cord or in bulb in nuclei of posterior columns or arcuate and lateral reticular nuclei) to the vermis and from the vestibule to the vermis, which are largely or entirely intact. In the same way the great efferent path from the cerebellar hemispheres, the dentato-rubral path is affected greatly while the fastigio-bulbar path, more especially from the vermis, is not so much involved.

It is obvious that such a case throws no light upon the direction of the paths involved, i.e., whether cerebello-petal or cerebellofugal, for we are not dealing with a secondary degeneration but with an atrophy or perhaps better an agenesia of correlated parts. This is well illustrated by the defects in the afferent and efferent paths, consisting of more than one system of neurones, to and from the left cerebellar hemisphere.

3. Various abnormal bundles of fibers were found in parts of the central gray, also abnormal masses of gray in the tegmentum of the pons and aberrant pontile fibers in certain parts of the tegmentum.

4. The absence of large masses of gray and of large bundles of fibers, such as the left superior cerebellar peduncle has caused in places a spatial readjustment of normal parts, exaggerating often the asymmetry of the two sides.

FIGURES

GENERAL KEY TO FIGURES

1, Nodule of abnormal cerebellar cortex
2, Right posterior horn
3, Left dorsal spino-cerebellar tract
4, Right nucleus cuneatus
5, Right nucleus gracilis
6, Right external nucleus of column of Burdach
7, Lateral external arcuate fibers
8, Left nucleus arcuatus
9, Left medial accessory inferior olivary nucleus
10, Left principal inferior olivary nucleus
11, Aberrant pyramidal bundles
12, Right medial accessory inferior olivary nucleus
13, Right principal inferior olivary nucleus
14, Left dorsal accessory inferior olivary nucleus
15, Transverse fillet fibers
16, Transverse olivo-cerebellar fibers from left olive to right restiform body
17, Lateral pyramidal bundles
18, Left external nucleus of column of Burdach
19, Left restiform body
20, Right restiform body
21, Left juxta-restiform body
22, Right juxta-restiform body
23, Medial longitudinal fasciculi
24, Ventral cochlear nucleus
25, Cochlear root of eighth nerve
26, Trapezius fibers
27, Spinal trigeminal root
28, Left cerebellar hemisphere
29, Left pontile nucleus
30, Transverse pontile fibers
31, Right middle cerebellar peduncle (right brachium pontis)
32, Left middle cerebellar peduncle (left brachium pontis)
33, Left central tegmental tract
34, Medial lemniscus
35, Vestibular root of eighth nerve
36, Facial nerve
37, Left nucleus dentatus
38, Abnormal gray masses in left ventral tegmentum and right reticular formation
39, Abnormal fiber bundles in right central gray
40, Aberrant pontile fibers
41, Superior olivary nucleus
42, Right superior cerebellar peduncle
43, Right mesencephalic trigeminal root
44, Left superior cerebellar peduncle
45, Left lateral lemniscus
46, Right lateral lemniscus
47, Left mesencephalic trigeminal root
48, Right central tegmental tract
49, Abnormal fibers in left central gray
50, Inferior colliculus
51, Left pes pedunculi
52, Right pes pedunculi
53, Left substantia nigra
54, Right substantia nigra
55, Abnormal fibers in dorsal central gray
56, Left nucleus ruber

All the figures are reproductions of photographs. In all figures of sections, except figure 6, the left side of the brain corresponds to the left side of the figure. In figure 6 it is reversed.

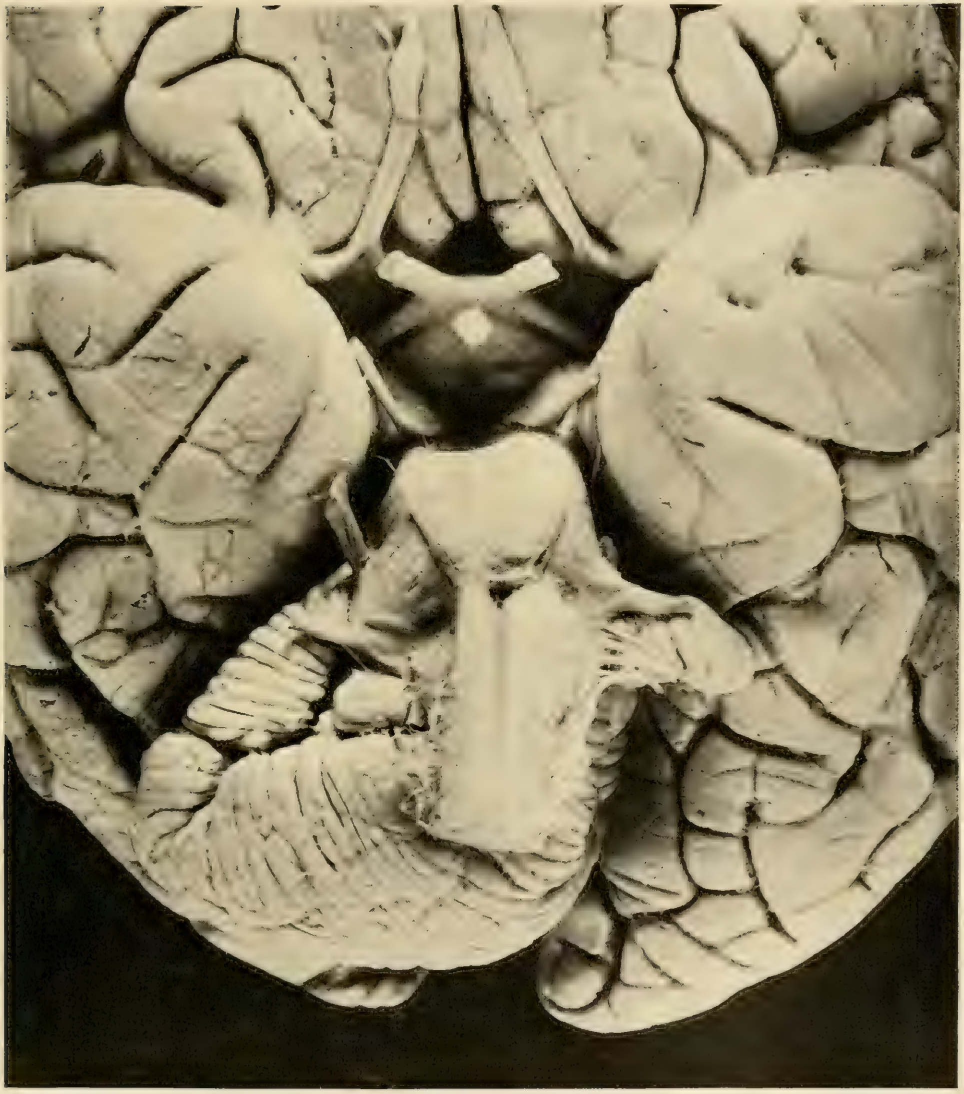
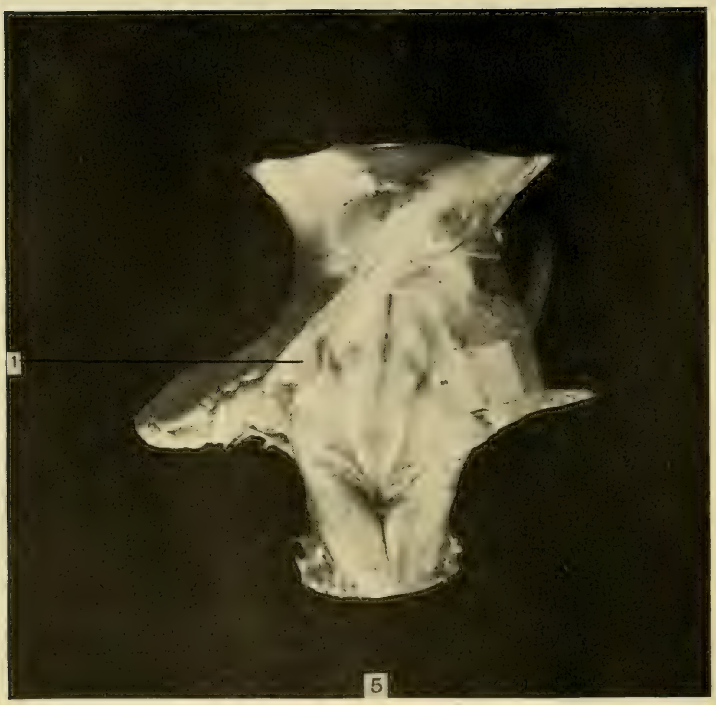


Fig. 1 Ventral view of a portion of the brain.

Fig. 2 Oblique ventro-lateral view of the brain from the left.

Fig. 3 Left lateral view of the cerebellum.
Fig. 4 Caudal view of the transversely cut cerebellum.



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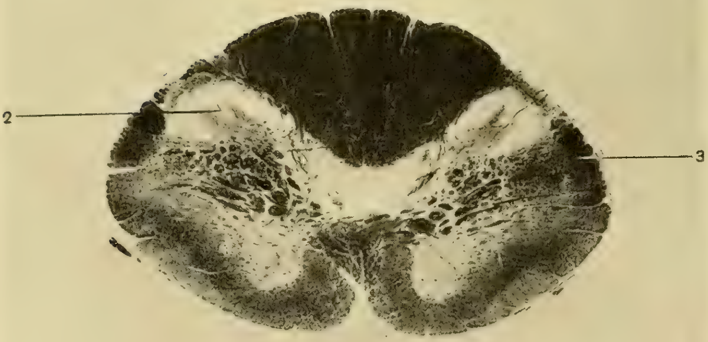

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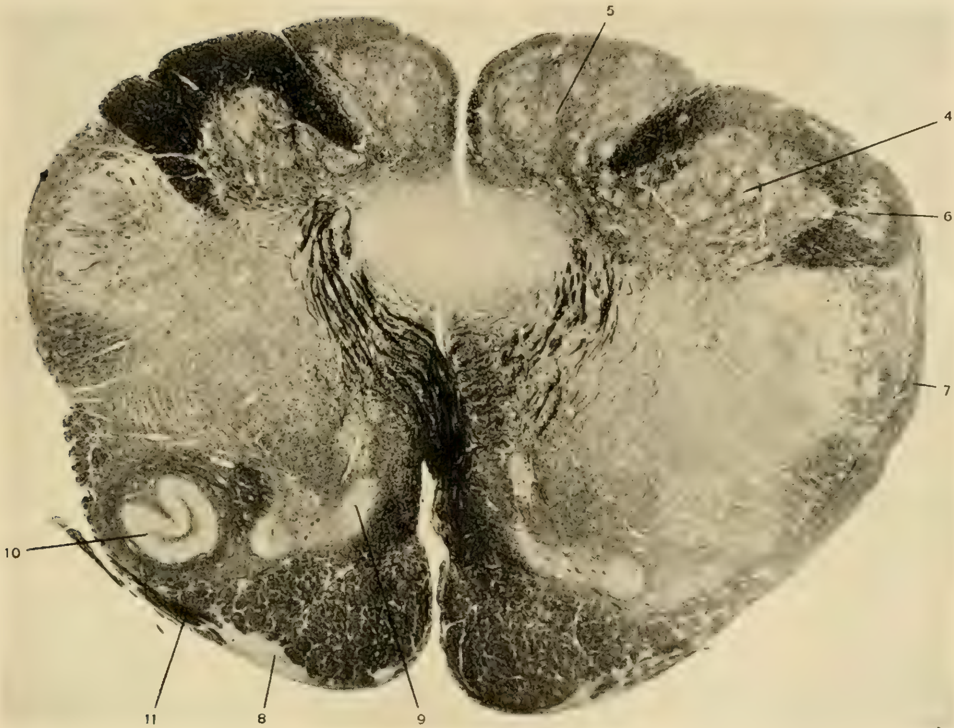

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Fig. 5 Dorsal view of bulb and midbrain, cerebellum removed. *1*, nodule of abnormal cerebellar cortex.

Fig. 6 Transverse section through the upper cervical cord. Weigert-Pal. *2*, right posterior horn; *3*, left dorsal spino-cerebellar tract.

Fig. 7 Transverse section through the bulb at the caudal extremity of the inferior olivary nucleus. Weigert-Pal. *4*, right nucleus cuneatus; *5*, right nucleus gracilis; *6*, right external nucleus of column of Burdach; *7*, lateral external arcuate fibers; *8*, left nucleus arcuatus; *9*, left medial accessory inferior olivary nucleus; *10*, left principal inferior olivary nucleus; *11*, aberrant pyramidal bundle.

Fig. 8 Transverse section through the bulb at the level of the lower middle part of the inferior olivary nucleus. Weigert-Pal. *9*, left medial accessory inferior olivary nucleus; *10*, left principal inferior olivary nucleus; *11*, aberrant pyramidal bundles; *12*, right medial accessory inferior olivary nucleus; *13*, right principal inferior olivary nucleus; *14*, left dorsal accessory inferior olivary nucleus; *15*, transverse fillet fibers; *16*, transverse olivo-cerebellar fibers from left olive to right restiform body; *17*, lateral pyramidal bundles; *18*, left external nucleus of column of Burdach; *19*, left restiform body; *20*, right restiform body.

Fig. 9 Transverse section through the bulb at the level of the emergence of the glossopharyngeal and cochlear nerves. Weigert-Pal. *10*, left principal inferior olivary nucleus; *11*, aberrant pyramidal bundles; *13*, right principal inferior olivary nucleus; *16*, transverse olivo-cerebellar fibers from left olive to right restiform body; *17*, lateral pyramidal bundles; *19*, left restiform body; *20*, right restiform body; *21*, left descending vestibular root and nucleus (left juxta-restiform body); *22*, right descending vestibular root and nucleus (right juxta-restiform body); *23*, medial longitudinal fasciculi; *24*, ventral cochlear nucleus; *27*, spinal trigeminal root.

Fig. 10 Transverse section through the bulb and caudal edge of the pons. Weigert-Pal. *11*, aberrant pyramidal bundle; *19*, left restiform body; *21*, left descending vestibular root and nucleus (left juxta-restiform body); *22*, right juxta-restiform body; *24*, ventral cochlear nucleus; *25*, cochlear root of eighth nerve; *26*, trapezius fibers; *27*, spinal trigeminal root; *28*, left cerebellar hemisphere; *29*, left pontile nucleus; *30*, transverse pontile fibers; *31*, right brachium pontis; *33*, left central tegmental tract; *34*, medial lemniscus.

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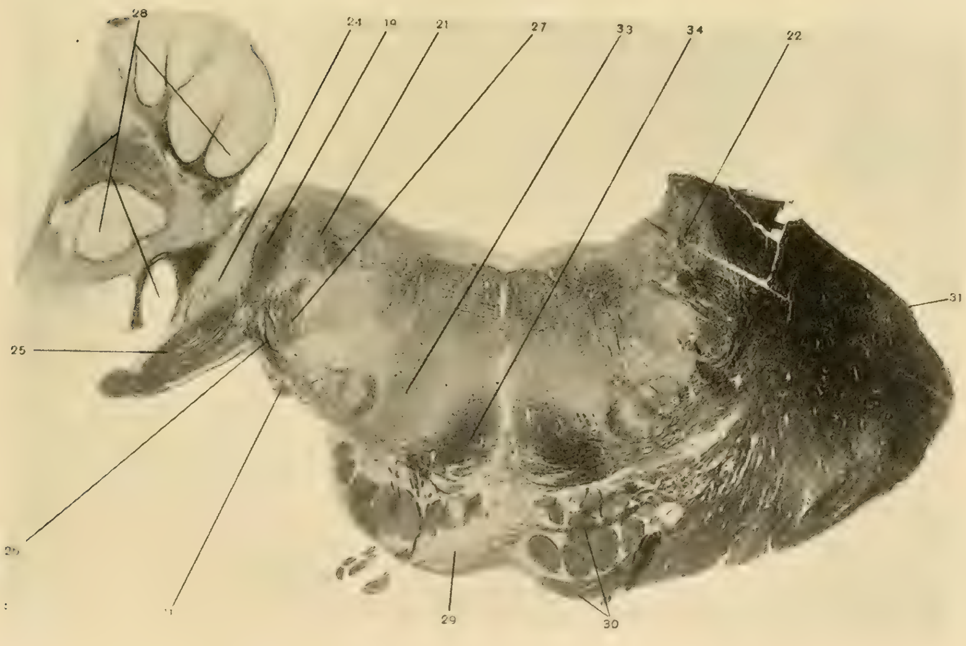

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Fig. 11 Portion of a transverse section somewhat cephalad to figure 10. Weigert-Pal. *11*, aberrant pyramidal bundle; *19*, left restiform body; *21*, left juxta-restiform body (vestibular root fibers and nuclei); *24*, ventral cochlear nucleus; *26*, trapezius fibers; *27*, spinal trigeminal root; *33*, left central tegmental tract; *35*, vestibular root of eighth nerve; *36*, facial nerve.

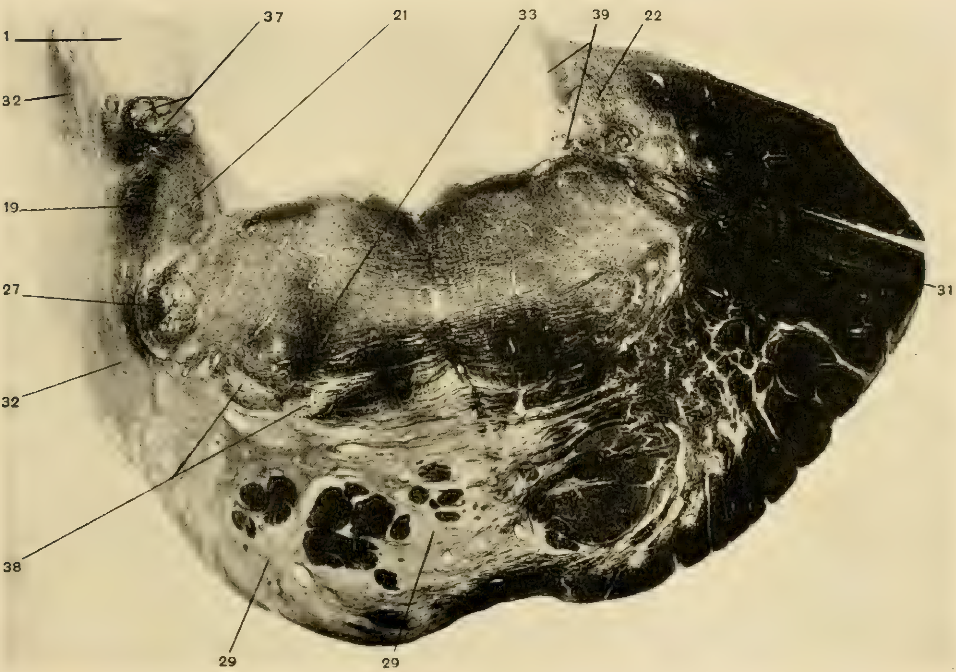
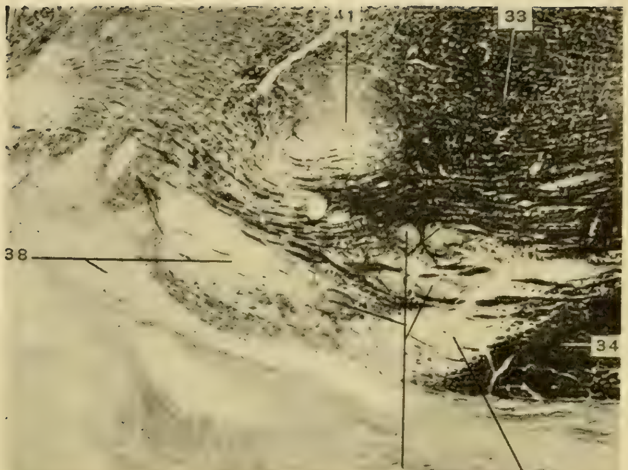


Fig. 12 Transverse section through the pons and pontile tegmentum just caudal to the emergence of the trigeminus. Weigert-Pal. *1*, nodule of abnormal cerebellar cortex; *19*, left restiform body; *21*, left juxtra-restiform body; *22*, right juxta-restiform body; *27*, spinal trigeminal root; *29*, left pontile nuclei; *31*, right middle cerebellar peduncle; *32*, left middle cerebellar peduncle; *33*, left central tegmental tract; *37*, left nucleus dentatus; *38*, abnormal gray masses in ventral tegmentum; *39*, abnormal fiber bundles in right central gray.



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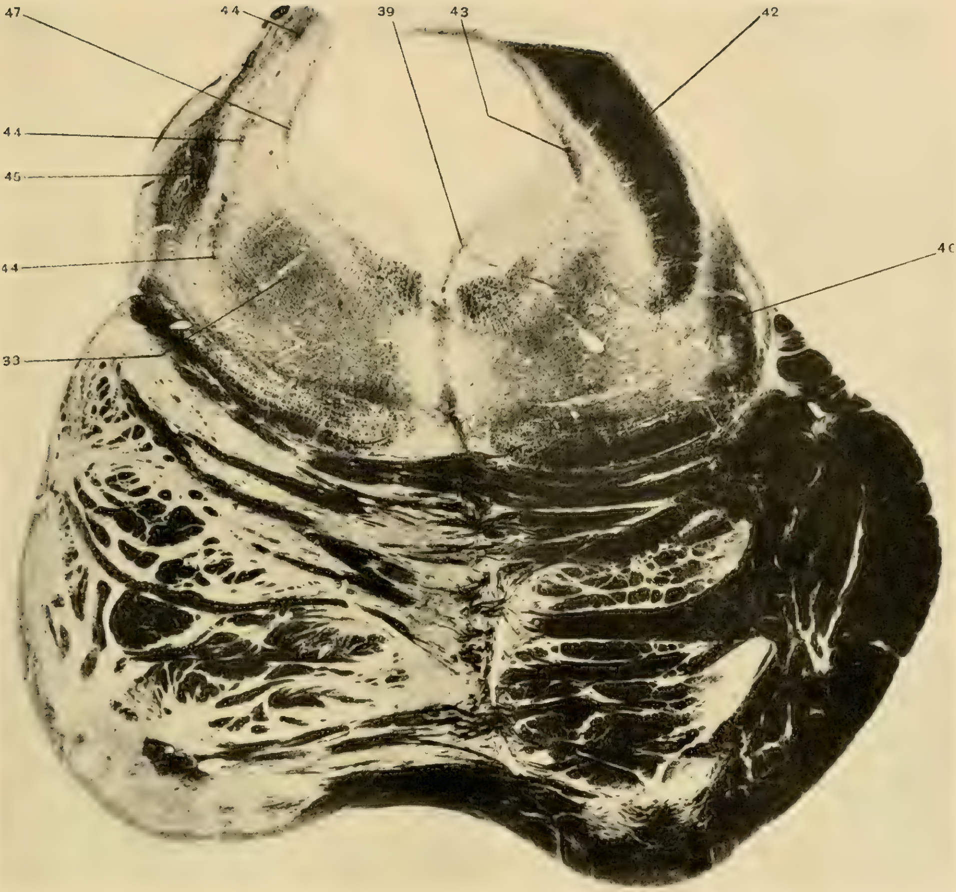

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Fig. 13 Portion of the preceding section more highly magnified. Weigert-Pal. *33*, left central tegmental tract; *34*, medial lemniscus; *38*, abnormal gray masses in ventral tegmentum; *40*, aberrant pontile fibers; *41*, superior olivary nucleus.

Fig. 14 Portion of a section a short distance caudal to figure 15. Weigert-Pal. *34*, medial lemniscus; *38*, abnormal masses of gray in right reticular formation; *39*, abnormal fiber bundles in right central gray and reticular formation; *42*, right superior cerebellar peduncle; *43*, right mesencephalic trigeminal root.

Fig. 15 Transverse section through the isthmus. Weigert-Pal. *33*, left central tegmental tract; *39*, abnormal fibers in right central gray; *42*, right superior cerebellar peduncle; *43*, right mesencephalic trigeminal root; *44*, left superior cerebellar peduncle; *45*, left lateral lemniscus; *46*, right lateral lemniscus; *47*, left mesencephalic trigeminal root.

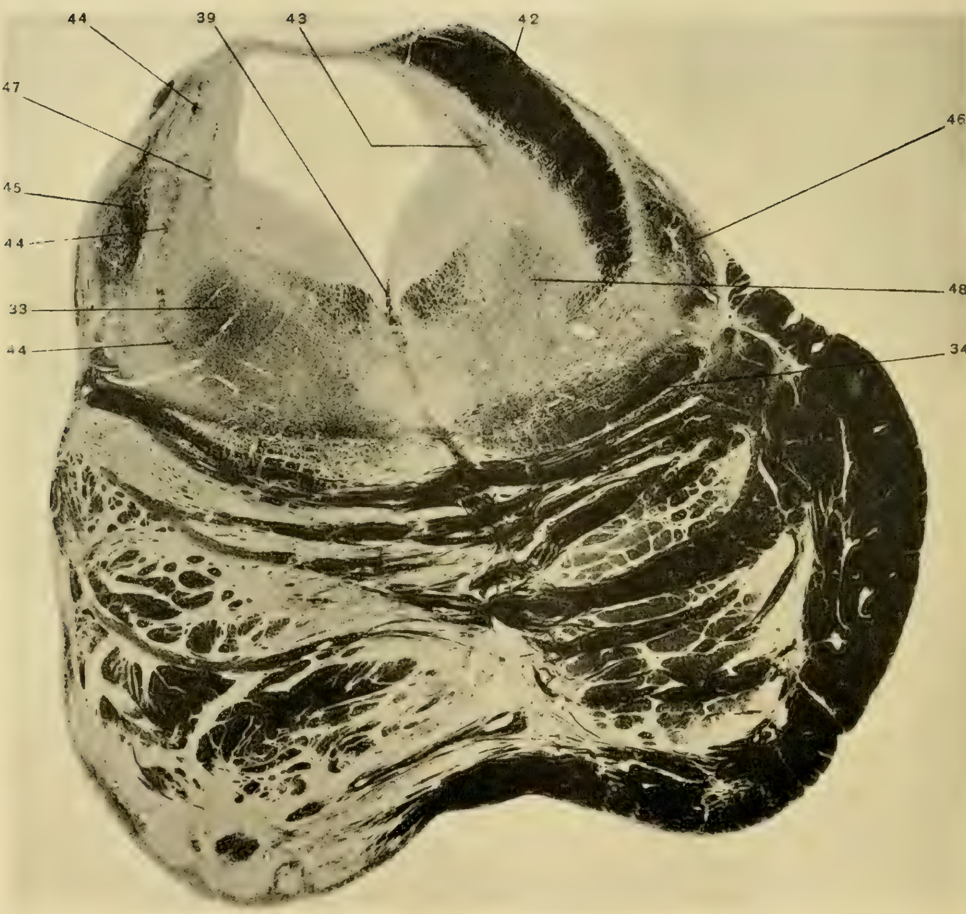


Fig. 16 Transverse section through the isthmus cephalad of figure 15. Weigert-Pal. *33*, left central tegmental tract; *34*, medial lemniscus; *39*, abnormal fibers in right central gray; *42*, right superior cerebellar peduncle; *43*, right mesencephalic trigeminal root; *44*, left superior cerebellar peduncle; *45*, left lateral lemniscus; *46*, right lateral lemniscus; *47*, left mesencephalic trigeminal root; *48*, right central tegmental tract.

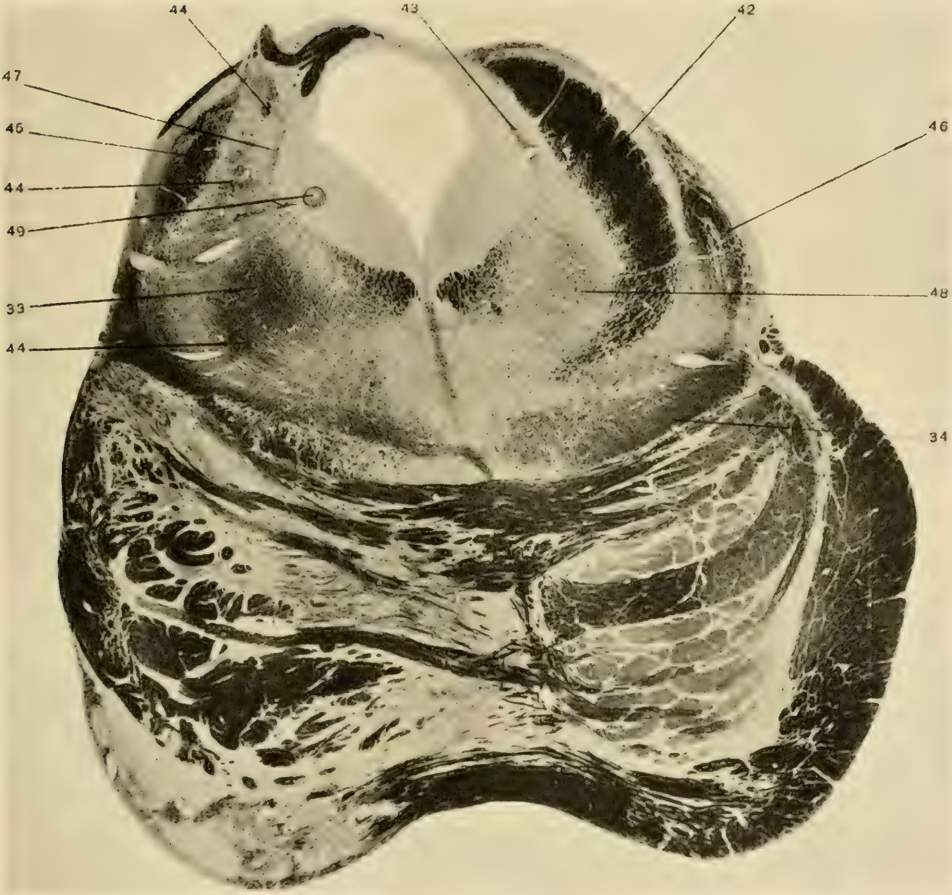
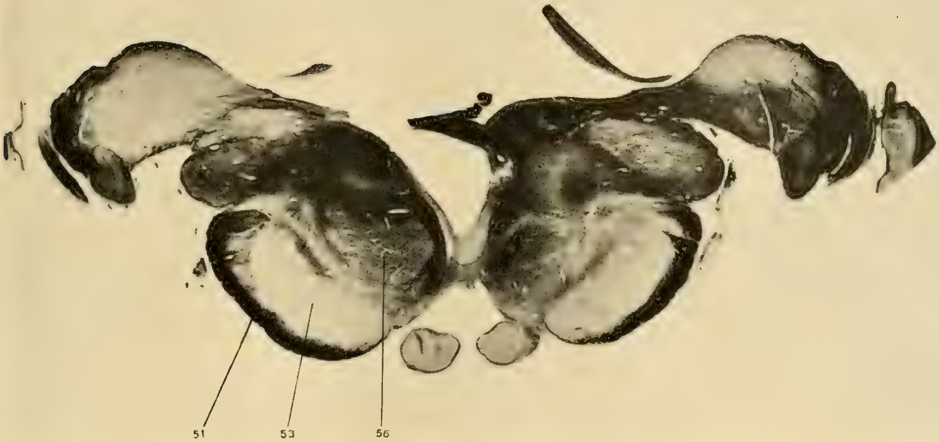


Fig. 17 Transverse section through the isthmus at the emergence of the fourth nerve. Weigert-Pal. *33*, left central tegmental tract; *34*, medial lemniscus; *42*; right superior cerebellar peduncle; *43*, right mesencephalic trigeminal root; *44*, left superior cerebellar peduncle; *45*, left lateral lemniscus; *46*, right lateral lemniscus; *47*, left mesencephalic trigeminal root; *48*, right central tegmental tract; *49*, abnormal fibers in left central gray.

Fig. 18 Transverse section through the level of the inferior colliculus. Weigert-Pal. *33*, left central tegmental tract; *34*, medial lemniscus; *42*, uncrossed, crossing and crossed fibers of the right superior cerebellar peduncle; *44*, some fibers of the left superior cerebellar peduncle; *50*, inferior colliculus; *51*, left pes pedunculi; *52*, right pes pedunculi; *53*, left substantia nigra; *54*, right substantia nigra; *55*, abnormal fibers in dorsal central gray.

Fig. 19 Transverse section at the junction of midbrain and thalamus. Weigert-Pal. *51*, left pes pedunculi; *53*, left substantia nigra; *56*, left nucleus ruber.

Fig. 20 Transverse section through the thalamus at the level of the optic chiasma. Weigert-Pal. *51*, left pes pedunculi; *56*, left nucleus ruber.



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THE CELL MASSES IN THE FOREBRAIN OF THE TURTLE, CISTUDO CAROLINA[1]

J. B. JOHNSTON

University of Minnesota

SIXTY FIGURES

In continuation of work upon the forebrain, it is the writer's intention to study the origin, growth and differentiation of the general pallium in the series of vertebrates. In doing this it will be necessary to keep constantly in mind the relations of the general pallium to the hippocampal formation, which has been described in earlier papers. The history of the amygdaloid complex and of the pyriform lobe is also intimately concerned. Finally, the position and arrangement of the fiber tracts connecting the hemispheres with the brain stem bear an important relation to the morphology of the cell masses in the forebrain.

In order to be able to compare given brain structures in lower and higher vertebrates it is necessary to have a description of the brain of some intermediate form in which the more common ichthyopsid characters can be recognized and in which at the same time the hippocampus and general pallium are present. For this purpose the brain of the turtle has been chosen and it serves admirably because of the relationship of the chelonia to the ancestors of mammals. The present paper will be confined almost wholly to description, the review of literature and the discussion of hypotheses being deferred to later papers.

METHODS

The results here presented have been obtained chiefly from the study of cell preparations. The results from the study of fiber tracts, although used in connection with this work, will be reported only briefly. The object has been to define the aggre-

[1] Neurological Studies, University of Minnesota, No. 21, July 20, 1915.

gations of neurones which there is reason to think are concerned with specific functions and to determine the position, extent and limits of these cell masses. Criteria depended upon are the position, size, form and grouping of the cells, their relation to fiber tracts and their relation to neighboring cell-masses. The more important aggregations of neurones are either separated from neighboring masses by cell-free zones, or they present a sudden transition to other masses whose cells differ markedly in size, position, staining qualities, etc. Sometimes sulci mark the lines of demarcation. Typical sections have been drawn to show the arrangement of cells in various regions and the lines of demarcation between the aggregations of neurones. To gain an understanding of the morphological relations, dissection and modelling have been practiced. After the various cell masses had been studied and their limits determined, a model was made of the right hemisphere together with a small adjacent part of the diencephalon. In making the plates for this model the limits of the several cell-masses were drawn under the projection microscope. The plates were then cut along these limiting lines but the parts not separated from one another. The model was then piled and fastened together as a whole and the several parts separated at last along the lines of the cuts. In this manner it was possible to pile the model accurately in the form of the control brain and since each part was strongly fastened together there was no distortion of the parts.

I am indebted to Dr. Wm. F. Allen for the beautiful photographs of this model.

DESCRIPTION

As is well known, the turtle has fairly large hemispheres whose caudal poles lie at the sides of the mesencephalon. The disposition of the hippocampal formation and the olfactory tubercle in the medial wall have been described in a previous paper. Other features in this wall will be taken up in later sections. The lateral wall shows a broad depression where the hemisphere connects with the brain stem which at once suggests comparison with the insular region in the mammalian brain (fig. 1).

The dorsal border of this depression is formed by a low ridge which extends rostrally into the lateral wall of the olfactory bulb. This ridge is traversed by the lateral olfactory tract and is therefore to be compared with the pyriform lobe of the mammalian brain. Near its rostral end it presents an apparent thickening which causes a decided elevation of the surface (figs. 5, 26). The sulcus which bounds the pyriform lobe dorso-laterally varies in depth in different individuals, but is always well marked in its rostral portion. It is the fissura rhinalis.

The insula-like region is clearly seen in the entire brain to be trasversed by bundles of medullated fibers (fig. 1). Sections show these to be a continuation of the crus cerebri (figs. 32, 49), and therefore comparable to the capsula interna. The absence of a cortical layer covering the internal capsule shows that this does not correspond to the insula. It is the corpus striatum which retains a condition analogous to that seen in the fish brain and is not yet covered in by pallium.

Caudal to the striatum there is a well-developed occipito-temporal pole whose presence adds to the similitude of the turtle's brain to that of a mammal. The pyriform lobe appears to blend with the occipital lobe. Along its lower border is a groove which at the rostral end is the sulcus endorhinalis. Behind the striated area a deep groove continues for some distance toward the caudal pole. This groove will be called the fissura amygdaloidea. A part of the area appearing below it in lateral view is occupied by the amygdaloid complex (fig. 5). The reason for calling this the amygdaloid fissure, however, is that it represents the line of infolding of an important body which becomes in mammals a part of the amygdaloid complex.

Rostral to the striated area appears the smooth lateral surface of the tuberculum olfactorium and adjacent olfactory area, including the lateral portion of the homologue of the anterior perforate space. Between this region and the pyriform lobe rostral to the striatum is the sulcus endorhinalis (figs. 19 to 26).

The vault of the hemisphere is occupied, as we shall see, by the general pallium. It is very evident that if the expansion of the general pallium were to push the pyriform lobe ventro-later-

ally until it was driven down nearly upon the basal surface and until the migrated general pallium itself had covered over the striatum, there would be produced a fairly exact counterpart of the primitive mammalian brain. This is the condition of the brain of an opossum or rabbit, in both of which the lateral (Sylvian) fissure is little deeper than the analogous striatal depression in the turtle's brain. The further expansion of the frontal and caudal poles produces the opercula bounding the lateral fissure.

On the dorsal surface just behind the olfactory peduncle occurs a slight rounded elevation (figs. 3, 25) which forms a part of the pallial thickening to be described below.

On the medial surface of a brain from which the stem has been cut away and the choroid plexus removed (fig. 3) it is seen that a wide chorioid fissure extends caudad in a simple curve from the interventricular foramen into the temporal pole. On removing the medial wall of the hemisphere there are exposed certain ridges which constitute some of the most characteristic features of the reptilian brain (figs. 4, 10). Three main bodies are to be distinguished: a *dorsal ventricular ridge*, the largest and most prominent; beneath it and extending farther rostrad, the *striatum;* and rostrally in the dorsal wall a smaller *pallial thickening.*

Three longitudinal ventricular grooves are to be distinguished: dorsal, middle and ventral. The dorsal ventricular groove is a very deep groove between the dorsal ridge and the pallium (figs. 4, 11 to 22). The middle groove runs beneath the dorsal ridge from the amygdaloid region forward into the olfactory bulb. A bifurcation of the caudal end of this groove and its significance will be mentioned later. The ventral groove is medial to the striatum. It dips very deep into the olfactory tubercle but is shallow rostral and caudal to this level.

The term epistriatum was first used by Edinger to designate a body in the reptilian forebrain to which C. L. Herrick had traced a large part of the olfactory tract. In the 1904 edition of Edinger's textbook this body is labelled epistriatum in figures 117, Varanus; 122 and 123, Schemata; 125b, lizard. This usage is followed by de Lange in a recent paper on Varanus. In Edin-

ger's figure 121 the term epistriatum is applied to an entirely different body in the turtle, the dorsal ventricular ridge of the present paper. In figure 125a, which also represents the turtle, this ridge is called mesostriatum and the term epistriatum is applied to the pallial thickening. Since the structure to which the term epistriatum was first applied does not appear as a special body or ridge in the turtle brain and since the author of the term uses it for at least three different bodies in the reptilian brain, the term will not be used in the present paper. The use of purely descriptive terms will help to avoid confusion.

In the dissected brain or in the model from which the hippocampal formation has been removed (figs. 4, 10) it is seen that the dorsal ventricular ridge bends down into the temporal pole. Here it enters into close relations with the amygdaloid complex which must be discussed later.

FORMATIO OLFACTORIA

The formatio olfactoria is that portion of the forebrain which receives fila olfactoria and contains mitral cells and glomeruli. It forms the rostral part of the olfactory bulb and extends farther caudally on the dorsal than on the ventral surface. Thus the peduncular constriction is placed obliquely, as is evident in figures 3 and 5. The bulb in its rostral part is nearly triangular in cross section (fig. 30). The olfactory nerve divides into distinct ventral and dorsal roots. The ventral spreads upon the dorsal surface of the bulb and enters the brain farther rostrally than does the dorsal root. The ventral root spreads over somewhat more than the lower half of the medial and lateral walls (fig. 30) and the rostral surface. The dorsal root continues over the bulb as a high ridge and spreads out in the dorsal wall in its caudal part. At its greatest extent, near the peduncle, this root extends half way down on the medial and lateral surfaces. The areas in which bundles of fila olfactoria are evident are shown in figures 28, 29, 30. It is certain, however, that many fila extend either in small bundles or singly some distance beyond these limits before ending in relation with neurones of the formatio olfactoria.

The limits of the formatio olfactoria can be determined more accurately by a study of the form, size and grouping of the cells. Throughout all the area where fila olfactoria are visible, the wall of the bulb consists of a thick layer of granule cells adjacent to the ventricle, and a fiber layer of varying thickness in the midst of which are scattered large and small mitral cells. In the areas not covered by bundles of fila olfactoria the mitral cells are less numerous and sometimes absent (figs. 28, 29, 30).

The deep granule cells are very numerous, closely crowded and sometimes arranged in irregular concentric layers. Golgi sections show that they possess two or more long slender dendrites radially placed and that the dendrites interlace with those of the mitral cells in the glomeruli. These cells are therefore true olfactory receptive cells, comparable to the deep cells of the olfactory formation of fishes (Johnston '01). The granule cells form a dense thick layer surrounding the ventricle throughout the whole extent of the bulb (figs. 28, 29, 30) and constitute the greater part of its volume. The groove or constriction which marks the olfactory peduncle follows accurately the caudal border of this granule cell layer. In the lateral wall the pyriform lobe and the olfactory tubercle push forward somewhat and the peduncular groove presents a V-shaped bend forward (fig. 5), but everywhere the groove faithfully indicates the boundary between primary or bulbar structure and the secondary centers or olfactory lobe.

The layer of mitral cells and of small brush cells is not as extensive as that of granule cells. In the rostral half of the bulb this layer is continuous around the periphery of the section, but the cells are less numerous in the lateral and medial angles where the fila olfactoria are not evident. In the caudal part of the bulb the corresponding areas become quite free from mitral cells for some distance (fig. 29, 31). The distribution of the mitral cells is determined by their relation to the fila olfactoria. Golgi preparations show that the dendrites of mitral cells and of the small brush cells penetrate the bundles of fila and ramify richly, thus transforming the bundles into elongated glomeruli or series of glomeruli. A brush often lies on the surface of one of these

bundles and its dendrites wrap around and penetrate the bundle. The formation of glomeruli in the course of large bundles of fila is a condition similar to that in Petromyzon described by the writer (1902). In addition to these large glomeruli are numerous smaller ones formed by the dendrites of small brush cells and of granule cells.

The formatio olfactoria consists then of (1) an enormous number of granule cells whose bodies form the dense peri-ventricular layers and whose rather straight dendrites radiate outward to form glomeruli or to mingle with dendrites of other cells in glomeruli; (2) a peripheral layer of mitral cells and small brush cells presenting a great variety of forms, whose dendrites form the large glomeruli by ramifying in the bundles of fila olfactoria; and (3) of the incoming fila olfactoria and the afferent and efferent fibers connecting the bulb with the rest of the brain.

The gross structure known as the olfactory bulb in the turtle consists of formatio olfactoria and nothing else. While the hippocampal formation and the pyriform lobe both push forward into close contact with the olfactory formation, the groove which marks the peduncle corresponds accurately to the line of division in the internal structure. The so-called nucleus olfactorius anterior in this brain is very clearly distinct from the granule cell layer of the olfactory bulb and does not extend forward beyond the peduncular constriction.

TRACTUS OLFACTORIUS

At the olfactory peduncle the fibers of the olfactory tract (figs. 55, 56, 57) have the following disposition. The largest bundles lie on the lateral surface and pass caudad into the pyriform lobe. These fibers arise from the greater part of the lateral and from the dorsal surface of the bulb. On the dorsal surface of the peduncle a large bundle, which has its origin in the dorsal part of the medial wall, crosses obliquely from the medial to the lateral surface and joins the bundle last mentioned. These constitute the lateral olfactory tract. Its further course will be described in connection with the pyriform lobe. Fibers arising from the remaining ventral and medial parts of the bulb col-

lect into a broad sheet ventral to the large bundle first mentioned. This sheet constitutes the medial olfactory tract. It is thick where it abuts upon the large lateral tract but spreads as a very thin sheet over the ventral and part of the medial surface. This tract runs caudad over the ventro-lateral surface of the tuberculum, gradually diverges from the lateral tract and gives diffuse fibers to the tuberculum and the parolfactory area. The medial tract borders the striatal area in front and below as the lateral tract borders that area dorsally.

Two compact terminal bundles of the medial tract are of especial importance. One bends up into the medial wall between the tuberculum and the commissures and is distributed to this region (gyrus subcallosus) and to the hippocampal formation. This is obviously the equivalent of the olfactory tract component in the precommissural fornix system of mammals. The second bundle continues along the lateral border of the medial tract and runs directly caudad to the amygdaloid prominence, where it enters the nucleus of small cells hereafter to be described as the nucleus of the lateral olfactory tract. This bundle runs along with the large bundle which connects the amygdaloid complex with the hippocampus through the precommissural system (olfactory radiations of Zuckerkandl or fiber bundle of the diagonal band of Broca).

CORPUS STRIATUM

Under this name will be described the structures which are homologous with the chief parts of the corpus striatum in human and mammalian brains. Attention has been called to the fibers of the crus cerebri which are seen in a depression on the lateral surface of the telencephalon. A section at the rostral border of this region (figs. 21, 34) shows two great bundles of fibers cut in cross section, the lateral forebrain bundle or crus and the medial forebrain bundle. The fibers of the crus rise in fascicles (internal capsule) scattered through the outer part of the thick latero-basal wall to the dorsal ventricular ridge and pallial thickening. These include somatic sensory fibers and probably also fibers descending to the motor centers. The medial bundle

consists of fibers which connect the olfactory centers with the hypothalamus and lower motor correlation centers. From this bundle fibers rise radially into the dense cell mass forming the floor of the ventricle (figs. 21 to 24, 34).

The whole mass in the latero-basal wall is the corpus striatum. It consists of two portions, a lateral much larger part containing large cells and a medial smaller part containing small cells (figs. 21, 22). The coarser fascicles of the crus rise in a curve through the lateral part into the dorsal ventricular ridge and the general pallium (figs. 32, 33). The finer fascicles of the medial bundle rise in almost straight lines radially in the rostral end of the medial part (fig. 34). In man the condensation of the pallial portion of the crus fibers into a plate-like internal capsule has taken place within a lateral large-celled area, the greater part of which is situated external to the capsule and is known as the lentiform nucleus. The remainder of the large cells together with a dense small celled area next the ventricle constitute the caudate nucleus.

In the turtle the large-celled and small-celled areas are clearly distinct from one another. The small-celled area will be called the caudate nucleus, the large-celled area the lentiform nucleus.

The caudate nucleus presents well marked head and tail portions. Far rostrad (fig. 26) this nucleus forms the floor of the ventricle between the ventral and middle ventricular grooves and occupies almost the entire thickness of the latero-basal wall. At its medial border it is continuous with the lateral parolfactory nucleus. This relation has been described for both reptiles and mammals in a previous paper ('13b, p. 389). Its basal surface is largely covered by the medial forebrain bundle from which fascicles enter the caudate. Followed rostrad in transverse sections the caudate is seen to be covered in by the layers of the olfactory tubercle which are continuous with the parolfactory area medially and the pyriform lobe laterally (fig. 27). In these layers are imbedded the olfactory tract fibers as elsewhere described. Continuing forward, the tuberculum and olfactory nuclei increase in thickness and the caudate grows smaller (fig. 28) until just behind the peduncle the caudate

disappears. It is this rostral end of the caudate nucleus that the writer identifies with the nucleus olfactorius anterior of Edinger and other authors. Following sections caudad, the sheet of olfactory fibers and cells scarcely disappear from the surface of the caudate until large cells appear in the lateral wall (fig. 26). Beneath the anterior end of the dorsal ventricular ridge this large-celled nucleus rapidly grows larger and the caudate smaller (figs. 22, 21) until the caudate is confined to a part of the floor of the ventricle adjacent to the ventral groove (fig. 20). From this point the tail of the caudate extends caudally to the point where the middle ventricular groove bifurcates (fig. 15, 10). Before this point is reached the caudate is in connection medially with the anterior nucleus region of the thalamus over the crus and the stria medullaris (figs. 17, 18). The caudate then grows thicker and merges insensibly with the small-celled mass of the amygdaloid complex (nucleus of the lateral olfactory tract) (figs. 15, 16). The caudate then disappears from the sections, its place being taken by an area of neuropile. Horizontal and sagittal sections show in this position a cell-free zone bounding the caudate behind, which corresponds to the ventral arm of the middle ventricular groove as it bends down into the temporal horn of the ventricle.

The caudate nucleus throughout its whole extent consists of small cells without regular arrangement. In its head portion it receives fibers from the olfactory tract and the medial forebrain bundle and gives fibers to the latter. In its tail portion are imbedded the stria terminalis and the great lateral olfactory projection tract of Cajal (figs. 48, 49).

A peculiar vesicular structure found in the head of the caudate and in the lateral parolfactory nucleus should be described here. The greater number of these structures are found around the depression of the ventricle which extends down into the tuberculum but some are found also in the lateral part of the caudate not far from the middle ventricular groove. At first sight these structures appear to be clusters of small cells arranged radially about a core somewhat like clusters of grapes about the stem. The clusters are elongated sometimes in the plane of transverse

sections, sometimes obliquely to it. In the latter case they may extend through as many as twelve sections ten microns in thickness. When the clusters are cut either across the long axis or lengthwise of it, the core is almost always seen to contain a lumen around which the cells are arranged (fig. 35). The lumen is bounded by a strong limiting membrane and contains more or less of lightly staining material, resembling mucus. Occasionally a flattened nucleus is seen in the lumen.

In the caudate and parolfactory nuclei these vesicles are found only near the ventricle except in the area where these two nuclei meet beneath the ventral ventricular groove. Here they are found farther from the ventricle, even in the deeper layer of the tuberculum olfactorium. In this region these vesicles lie adjacent to or intermingled with the islands of Calleja, to be described below. It was at first thought, indeed, that these were islands of a special type. The vesicular arrangement and other characters of the cells, however, differentiate these structures sharply from the islands of Calleja. The cells are typically columnar and radially arranged around the lumen, the nuclei usually placed near the peripheral end of the cells. The cell-bodies are often filled with small granules unlike the Nissl-bodies of adjacent nerve cells. The nuclei are small, ovoid and dense, resembling those of ependyma cells rather than those of nerve cells. There are often larger cells, obviously nervous, wedged in among or closely applied to the outer surface of the small cells of the vesicles. Although the fascicles of nerve fibers in the caudate often pass close over the surface of these vesicles and sometimes diffuse fibers appear to run ventrad from a vesicle, I have not found in Cajal or Golgi sections fibers arising from the cells of the vesicles.

I suspect that these vesicles are composed chiefly of ependyma cells and that their lumina represent vestiges of ventricular cavity which have been pinched off during development. This might happen owing to the thickening of the caudate and parolfactory nuclei and consequent encroachment upon the ventral part of the ventricle. The fact that these cell clusters are not penetrated by the neuropile (fig. 35) and the fact that no definite

fascicles of nerve fibers are found running to or from them, constitute negative evidence as to their nervous function. At the same time, nerve cells are often found closely related to or imbedded in the ependyma and further study will be necessary to determine the origin, character and significance of these structures.

THE LENTIFORM NUCLEUS

At its rostral end this nucleus appears simply as scattered large cells, outside of the small-celled caudate, among which fascicles rise from the crus to the pallial thickening in the rostral part of the roof. Beneath the rostral end of the dorsal ridge this nucleus has grown to a large body in the lateral wall and has reached the ventricle (figs. 22, 23). From this point caudad a peculiar band of thickened ependyma covers the ventricular surface of this nucleus (figs. 15 to 22, 36). This thick band extends some distance below the middle ventricular groove and bends round that groove into its dorsal wall. While the ependyma elsewhere in the lateral ventricle has from one to three rows of nuclei, this band consists of very tall cells and presents as many as seven to nine rows of nuclei. The peripheral processes of these cells are strong and give a prominent striation to the adjoining nucleus (figs. 36, 37). The curved course taken by these processes which come from the dorsal wall of the middle groove (fig. 37) shows that the groove was formed within the ependymal band and near the border of this nucleus. It also shows how the groove has been formed during the development of the individual by the pushing in of the dorsal ridge which forced this border of the nucleus to be bent over. This thickened ependyma extends right back into the dorsal branch of the middle ventricular groove, where it quickly disappears. Throughout its length this thickened band of ependyma covers a nucleus whose cells are distinctly larger and usually much more numerous than those of the adjoining caudate.

In the striatal area this nucleus makes up the whole thickness of the wall and is traversed by the fascicles of the crus as above noted. Toward the caudal border of the striatal depression

(figs. 17, 16) the lentiform nucleus becomes covered externally by a layer of small cells which reaches from the pyriform lobe to the amygdaloid complex and will be described below as the nucleus of the lateral olfactory tract. The lentiform nucleus now decreases in volume caudally, contains several dense collections of cells which are closely related to the thickened ependyma of the middle groove (figs. 16, 33), becomes less rich in cells and finally merges with the central core of the dorsal ventricular ridge behind the end of the middle groove (fig.14).

Throughout its whole length the lentiform nucleus is sharply delimited from the pyriform lobe and (except at its caudal end) from the dorsal ventricular ridge, by cell-free zones. It is marked off from the caudate only by a rather sudden change from large to small cells. The thickened ependyma covering its surface is sometimes separated from that covering the caudate by a slight, sharp groove.

Among the fascicles of the internal capsule which come from the sensory bundle of the crus (see later section on the pallium), are found many cells conspicuously larger than the ordinary cells of the lentiform nucleus. The position of these is indicated in figures 18 and 19. They may prove of importance in further comparisons with the mammalian brain.

TUBERCULUM OLFACTORIUM

The tuberculum consists of a cap of two layers of cells covering the basal surface of the caudate nucleus at its rostral end (fig. 27). The outer layer is sparsely filled with small cells and is closely related at its medial border with the medial parolfactory nucleus and at its lateral border with the pyriform lobe at the sulcus endorhinalis (figs. 26, 27). The inner layer has larger cells and is characterized by the grouping into islands which have been described by Calleja and Cajal. These islands are for the most part clusters of the large cells of the deep layer. They contain from four or five to many cells, which present no regularity of arrangement. The cell bodies are pear-shaped or stellate and are largely filled by vesicular nuclei with prominent nucleoli. In these respects they do not differ materially from the cells

scattered between the islands. Some of the cells in the islands take a lighter, more transparent and brilliant stain in neutral red than others.

In addition to the islands of large cells there are a number of dense clusters of small cells which are undoubtedly nerve cells. These clusters do not present a core or lumen and the neuropile does not shrink away leaving a clear space around them as happens in the case of the vesicles described in the caudate nucleus. The true islands are confined to the deeper layer of the tuberculum. It must be noted, however, that the tuberculum extends into the medial wall and merges with the medial parolfactory nucleus. The distribution of the islands may arbitrarily be taken as determining the extent of the tuberculum. The greater number of islands is found near the mediobasal angle and they do not extend far laterally. Caudally the islands disappear from the basal surface where the medial forebrain bundle collects (fig. 24) and are found farther caudad in the medial wall.

There is a very close resemblance between the tuberculum olfactorium in the turtle and the 'superficial basal area' described by the writer in selachians (1911). The writer was unwilling at that time to give the name tuberculum olfactorium to this area because it seemed to include parts of the medial and lateral olfactory nuclei and the region corresponding to the anterior perforate space. The close relation of the tuberculum to medial and lateral olfactory nuclei is common throughout vertebrates and I shall present evidence at another time that the tuberculum and anterior perforate space are by no means wholly independent.

ANTERIOR PERFORATE SPACE

The area corresponding to the anterior perforate space of mammals is not sharply marked off in the turtle. It occupies the caudal part of the basal surface of the large rounded prominence rostral to the optic chiasma. The rostral half of this surface shows the characteristics of the olfactory tubercle. The caudal half lacks these peculiarities and is largely filled by the medial forebrain bundle.

DIAGONAL BAND OF BROCA AND GYRUS SUBCALLOSUS

The large basal mass which includes the head of the caudate, the parolfactory nuclei, the tuberculum olfactorium and the anterior perforate space appears on the medial surface as a rounded area (figs. 3, 6) bounded dorsally and caudally by a groove which descends to the basal surface, bends transversely, and disappears. This groove, as the further description will make clear, is the homologue of the fissura prima of His.

The area dorsal to the horizontal limb of this fissure is the primordium hippocampi (Johnston '13 b). The area between the fissure and the lamina terminalis (fig. 6, *g.s.*) is occupied by a cell mass and a fiber bundle both of which are characteristic of this region in all mammals and perhaps in all vertebrates. In a previous paper ('13 b) this cell mass has been included in the description of the medial nucleus parolfactorius in both the turtle and mammals. This was an error. Since this cell mass lies caudal to the fissura prima in mammals, it is outside the limits of the parolfactory area. It may be spoken of as the *nucleus of the diagonal band.* In mammals this consists of a thin plate of closely packed cells which extends from a point rostral to the anterior commissure down in front of the optic chiasma and caudad on the latero-basal surface to the amygdaloid complex. It is very sharply marked in the rabbit and has been figured in the opossum and bat ('13 b, figs. 28, 42). The distinction between this nucleus and the medial parolfactory nucleus is shown in figure 46 of the paper referred to, where this nucleus consists of small cells rostral to the anterior commissure and is not separately labelled. The cell-free zone between this and the medial parolfactory nucleus corresponds to the fissura prima.

In the turtle the same plate of cells is found (figs. 20, 21) occupying the medial surface rostral to the anterior commissure and extending down close in front of the preoptic recess, near the large-celled supraoptic nucleus (fig. 19), and continuing laterally and caudally ectal to the medial forebrain bundle (fig. 18) until it expands into the large anterior nucleus of the amygdaloid

complex from which arises the great olfactory projection tract (fig. 17). The relations to the amygdaloid will be further described in the next section. The extreme rostral and upper end of this nucleus is the very dense collection of cells seen near the recessus superior in figures 19 and 39. There is no break in the continuity of the nucleus described but on the basal surface in front of the optic chiasma and lateral to the optic tract, the number of cells is much less than in the medial wall. Throughout the length of the nucleus its cells are small and are somewhat elongated in the direction of the densely packed bundle of fine fibers among which they lie.

The fibers in question enter into the precommissural bundles of the fornix system in the medial wall. They are the olfactory radiations of Zuckerkandl and constitute the chief pathway from the amygdaloid region to the hippocampus. Compare '13 b, p. 410. From the amygdaloid forward along the basal surface these fibers form a low ridge parallel with the optic tract (figs. 1, 8, 19) and in this position the bundle is clearly visible in the entire brain (fig. 2). The bundle is clearly distinct from the medial forebrain bundle which lies ental to this. In front of the optic chiasma the bundle is seen to be composed of two parts, one of which is derived from the medial olfactory tract as above described, while the other bends up into the medial wall, spreads out in the area between the fissura prima and the commissures, and enters the hippocampus (figs. 56, 57). The triangular area between the fissura prima and the commissures in which this bundle spreads out like a fan is the equivalent of the mammalian gyrus subcallosus. Lateral to the optic chiasma this bundle passes close to the supra-optic nucleus and there seems to be a connection between the two which has not yet been carefully studied.

The homology of the area described in this section with the gyrus subcallosus and the diagonal band of the mammalian brain is obvious. Its chief morphological significance is that it represents the persistence of the preoptic and precommissural connection between the medial olfactory area and hippocampus on the one hand and the lateral olfactory area and amygdaloid

complex on the other hand. In the ichthyopsid brain where the temporal pole has not yet been formed, the continuity of the corresponding regions is broad and direct. The size and functional importance of this connection in reptiles and mammals is of great significance for the explanation of the evolution of the temporal pole and the general pallium.

LOBUS PYRIFORMIS

As already indicated the pyriform lobe forms a somewhat prominent ridge along the dorso-lateral surface of the hemisphere, extending from the olfactory peduncle into the caudal pole. It is separated from the general pallium dorsally by the fissura rhinalis. Rostrad this fissure runs obliquely mesad and joins the peduncular groove or constriction as it bends down into the medial wall. Caudally the fissura rhinalis presents considerable individual variation in its depth and length. Usually it fades away at about the middle of the hemisphere (fig. 1) so that there is no gross boundary line between the caudal part of the pyriform lobe and the general pallium. In the rostral part of the hemisphere a slight sulcus endorhinalis approximately marks the boundary between the pyriform lobe and the area occupied by the tuberculum and corpus striatum (figs. 22 to 26). The caudal continuation of this sulcus becomes much deeper between the pyriform lobe and the striatal area (fig. 1) and bends down between the striatal area and the amygdaloid prominence. At the point of bending is the deepest part of this groove and from this point the amygdaloid fissure extends caudad as above described.

The pyriform lobe consists of the lateral olfactory tract and the special gray matter accompanying the tract. Sections through the middle or rostral part of the lobe (figs. 19, 25) show that it consists of a superficial fiber layer and a deeper plate of cells and that it is everywhere very clearly and sharply separated from the border of the pallium, the dorsal ventricular ridge and the lenticular nucleus by a cell-free zone. This cell-free zone is more sharply marked than any other in the brain.

The outer surface of the lobe is covered by a continuous sheet of fibers of the lateral olfactory tract. These arise in larger part from the lateral wall of the olfactory bulb and in smaller part from the dorsal and medial wall. The former fibers enter the extreme rostral end of the pyriform lobe on the lateral surface of the peduncle; the latter cross from the medial to the lateral side in the peduncular groove on the dorsal surface and join the former fibers to make up the common tract (figs. 55, 56).

Just behind the peduncular constriction the pyriform lobe appears to thicken rapidly. This thickening forms a conspicuous rounded prominence on the dorso-lateral surface of the hemisphere (figs. 26, 5). The arrangement and relations of the cell masses in this prominence show at once that it is made up of two parts. The surface layer of cells belongs to the pyriform lobe and is no thicker here than elsewhere. The elevation here is due to the deep layer of cells which is the thickened lateral border of the general pallium (figs. 24, 25, 26). This is indeed a lateral extension of the dorsal pallial thickening, which lies beneath the pyriform lobe as the lateral border of the pallium does throughout the rostral two-thirds of the lobe. The pyriform lobe, then, is not actually thickened but is merely bulged out by the thickening of a pallial formation beneath.

The majority of cells in the pyriform lobe are large multipolar cells with large dendrites. In regard to this a comparison of the pyriform lobe with other parts of the forebrain reminds one of the comparison between Deiters' nucleus and adjacent nuclei in the medulla oblongata. The cells are noticeably larger in the rostral half of the lobe than in the caudal, the largest cells and the greatest proportion of large cells being found just behind the prominence above mentioned. In the caudal part the cells become distinctly smaller and where the lobe broadens out to form the lateral wall of the ventricle, the cells take on pyramidal forms much like the cells of the general pallium or the hippocampus.

Throughout the rostral half of the pyriform lobe small cells are almost wholly confined to its ventral portion (figs. 19, 25, 40). These small cells extend somewhat below the sulcus endorhinalis,

and the cell-free zone, which accurately marks the boundary of the lobe, meets the surface ventral to the sulcus endorhinalis. This sulcus is therefore actually within the area of the pyriform lobe. At the caudal border of the striatal area the band of small cells along the ventral border of the pyriform lobe spreads ventrad in a broad sheet across the base of the amygdaloid fissure (fig. 5) and expands into a large nucleus of small cells occupying the lateral and rostral part of the amygdaloid prominence (figs. 17, 16). This sheet of small cells is accompanied by a large bundle of fibers from the lateral olfactory tract which ends in this nucleus. This is the nucleus of the lateral olfactory tract (figs. 5, 17).

A further examination of the relations of the small cells in the pyriform lobe shows that essentially two nuclei or two cell groups are to be distinguished. The small cells in the region of the amygdaloid fissure are very clearly separated from the large-celled part of the lobe by a space or cell-free zone (figs. 15, 16, 17). Farther forward although there is no space separating them, the small cells do not mingle with the large cells and the small-celled band becomes continuous with the superficial layer of the tuberculum and through that with the medial olfactory nucleus (fig. 26). The large-celled nucleus, on the other hand, maintains its identity rostrad to the peduncle as already described (fig. 28). Moreover, the location of the small cells below the endorhinal sulcus gains significance from the fact that at the level of the tuberculum the small-celled band spreads ventrally to become continuous with the superficial layer of the tuberculum. The cell-free zone which limits the pyriform lobe internally now becomes continuous with the limiting zone which appears between the caudate sulcus and the layers of the tuberculum (figs. 26, 27).

These relations when summed up with the description that has gone before show that there is a continuous area of small-celled olfactory nuclei comprising the medial parolfactory nucleus, the superficial layer of the tuberculum, the small-celled band of the pyriform lobe, the small-celled nucleus of the amygdaloid complex and the nucleus of the diagonal band. These together constitute a continuous ring which surrounds the crucial-striatal area.

The whole of this ring receives fibers from either the lateral or medial olfactory tract. This continuous complex of small-celled nuclei seems to serve as an intermediate selecting and distributing station through which olfactory impulses are forwarded to the cortical center for sensation, the hippocampus; or to one of the motor correlation centers in the diencephalon, or to centers lower down the brain stem (compare Johnston '15 a). The greater part of the pyriform lobe made up of large cells is probably concerned with olfacto-somatic correlation. Other places for correlation of olfactory and somatic impressions are probably found in the amygdaloid complex and in the hippocampus (subiculum). The distribution of large cells in the pyriform lobe probably gains significance from their relation to the pallial thickening.

The boundary line between the pyriform lobe and the general pallium is less distinct in the caudal part than elsewhere. As the pyriform lobe is followed caudad in sections to the point where it forms the whole thickness of a part of the wall of the ventricle (figs. 13 to 15) the cell-free zone at first continues as a very clear oblique dividing line in this wall (fig. 14). This overlapping of the general pallium by the border of the pyriform lobe is very characteristic. This dorsal border of the lobe rises dorsally in its caudal portion as the model clearly shows (fig. 5). In transverse sections through the region in which the small-celled portion of the pyriform lobe spreads ventrad to merge with the nucleus of the lateral olfactory tract, the cell masses of the dorsal ventricular ridge begin to be connected by a thick curved layer of cells with what appears to be the cell layer of the pyriform lobe in the lateral wall (fig. 15). When this relation is studied in sections farther caudad (figs. 11, 12) it is clearly seen that it is the general pallium which thus enters into continuity with the ventricular ridge. In transverse sections there is no sharp boundary between pyriform lobe and general pallium. It is noticed, however, that there is a narrow portion of the wall adjacent to the dorsal boundary of the lobe in which the cells are placed close to the ventricular surface (fig. 12). The oblique line bounding the lobe dorsally at length gives way to a narrow

area in which the cells of the lobe meet those of the pallium above in a confused mass. The ventro-caudal margin is not clear. Sections give the impression that the pyriform lobe merges insensibly with the general pallium in this region. In the model this boundary has been fixed arbitrarily.

THE AMYGDALOID COMPLEX

When the hemisphere of the turtle brain is viewed from the lateral and basal aspects (figs. 1, 2, 5, 6) the region which is occupied in part by the amygdaloid complex appears as a basal prominence similar to the temporal pole of the mammalian brain. It is bounded rostrally by the crucial-striatal area, medially by the optic tract and thalamus and laterally by the amygdaloid fissure. Caudally this prominence passes insensibly into the rounded caudal pole.

Nucleus of the lateral olfactory tract. As above described, a part of the lateral olfactory tract bends down across the amygdaloid fissure just caudal to the striatal area and ends in the lateral border and rostral tip of the amygdaloid prominence (fig. 8). This region is therefore clearly homologous with the nucleus of the lateral olfactory tract in the mammalian brain. This nucleus is composed of small cells which occupy the tip and lateral part of the amygdaloid prominence and extend in a thin layer across the amygdaloid fissure to meet in a thickened border the large-celled nucleus of the pyriform lobe (figs. 16, 17). The two nuclei are separated by a cell-free zone and this condition continues back to the end of the nucleus (fig. 13). At the caudal border of the striatal area the thin layer of small cells is traversed by the fibers of the lateral olfactory tract which bend down into this nucleus, and by numerous fibers from the pyriform lobe which pass over the surface of the nucleus to join the stria medullaris (fig. 56). From the tip of the amygdaloid prominence the fibers of the diagonal band go forward as above described. These are also mingled with the stria medullaris. At the same time the small cells of the diagonal band merge with the small-celled nucleus of the lateral olfactory tract (fig. 17).

Where the thin layer of small cells forms the boundary of the striatal area it covers in the large-celled lateral nucleus of the corpus striatum (nucleus lentiformis) (fig. 16). In transverse sections the nucleus lentiformis is followed caudad for some distance beyond this, always traversed by bundles of crucial fibers which are bending up into the pallium and the dorsal ventricular ridge. The nucleus lentiformis gradually grows smaller and is replaced by the small-celled nucleus which grows thicker caudally and enters into close relations with the caudate nucleus. Indeed, in its rostral portion the entire amygdaloid eminence is filled with small cells, the ventricular portion being the caudate nucleus, the superficial portion being the enlarged continuation of the nucleus of the lateral olfactory tract (fig. 17).

Relations of the caudate nucleus. It has been stated that the caudate ends about opposite the end of the middle ventricular groove and is bounded by the branch of that groove which bends down into the temporal horn of the ventricle. Here the caudate merges with the nucleus of the lateral olfactory tract in a small-celled mass which constitutes the chief part of the amygdaloid complex. In the lizards this mass, or the caudate part of it, is greatly enlarged and forms a prominent lobe or ridge in the ventricle. C. L. Herrick showed that this was an important olfactory center and it is this lobe which was first called epistriatum by Edinger. It was this body whose relations very naturally suggested to Kappers ('08) that the epistriatum of lower vertebrates formed or entered into the amygdaloid complex of mammals. In the turtle this body is simply a part of the amygdaloid complex without hypertrophy. However, if all the other structures to which the term epistriatum has been applied were to be gathered into it, the amygdaloid complex would be a veritable museum!

The caudate nucleus at its rostral end is closely related to the olfactory tubercle and parolfactory area and receives fibers from the medial olfactory tract. At its caudal end it enters into close relations with the nucleus of the lateral olfactory tract and helps to form the olfactory part of the amygdaloid complex.

Medial large-celled nucleus. In sections through the rostral part of the amygdaloid complex the small-celled mass is covered basally by a rounded cap consisting almost wholly of neuropile (figs. 16, 42), only a few medium sized cells being imbedded in it. This neuropile is formed by the interlacing stria medullaris, lateral olfactory tract and olfactory radiations as above described. As the sections are followed caudally the cells in this neuropile increase in number and size until a conspicuous nucleus forms the basal portion of the complex (figs. 15, 43). This is the condition in sections which pass through the caudal border of the stria medullaris. Just caudal to this (figs. 14, 44) the temporal horn of the ventricle penetrates this nucleus. Farther caudally the large cells are all found in the lateral or amygdaloid wall of the ventricle while the hippocampal formation and fimbria appear in the medial wall. The large-celled nucleus lies ventral to the tail of the caudate nucleus. This is the region in which the tail of the caudate merges with the small-celled nucleus of the lateral olfactory tract. Following the sections caudad, the caudate rapidly diminishes and the large-celled nucleus spreads farther dorsad in the large ventricular ridge (figs. 13, 45). At the same time the nucleus of the lateral olfactory tract grows smaller and appears as a rather dense mass of cells near the amygdaloid fissure. Now there appears in the ventral wall between this and the hippocampus an area of scattered cells which on being followed further caudad is found to belong to the general pallium (which see). By the time this condition is reached the caudate has entirely disappeared from the sections and the large-celled nucleus has spread dorsad to the level of the dorsal branch of the middle ventricular groove. Here this nucleus constitutes a ventricular layer of large cells rather closely packed but not arranged in clusters as are the cells of the dorsal part of the dorsal ventricular ridge. Further from the ventricle the lower part of the ridge is filled by the same irregularly placed cells as are found in the dorsal part. Both these and the ventricular layer of large cells merge with the general pallium in the ventral wall. The ventricular layer representing the large-

celled nucleus continues over the medial surface of the basal lobe of the ridge to its caudal end.

Further evidence as to the individuality of this nucleus is found in its fiber connections. Only the general disposition of its chief tract will be described here. In the extreme tip of the temporal horn of the ventricle (figs. 10, 13, 14) is seen a small ridge which follows the ventro-rostral border of this nucleus. It is clearly seen in the model and in sections in all planes. This ridge is composed chiefly of fibers which run caudad over the medial surface of this nucleus. In addition to the bundle which forms the ridge there is a thin sheet of fibers in small fascicles covering the whole medial face of this nucleus. All of these fibers gradually disappear as they are traced caudad over this nucleus, in which they have either their origin or ending. Traced rostrad all these fibers pass through the tail of the caudate as a thick bundle. Here the bundle is just lateral (internal) to the stria medullaris as that bundle rises from the nucleus of the lateral olfactory tract to enter the thalamus. The bundle here described now forms the most compact part of the stria terminalis and in addition a large part of its fibers go forward diffusely in the substance of the caudate nucleus. A further discussion of the relations of this bundle will be reserved for a later study of the stria terminalis system. It is evident, however, from the facts given, that what is here described as the medial large-celled nucleus belongs to the amygdaloid complex and the distribution of the stria terminalis bundle confirms the observations as to its extent, based upon the character and grouping of cells.

Dorsal ventricular ridge. Farther caudally in transverse sections the ventricle pushes around both laterally and ventrally until the whole ventricular ridge is seen attached to a pallial wall and no longer to the brain stem (figs. 11, 12). In this pallial wall the extent of the general pallium and hippocampal formation can be made out, at least roughly, as represented in the model. The dense, deep layer of cells of the pallium turns into the ventricular ridge where it is continued by layers of cells lying adjacent to the ventricle. The sparsely scattered cells in the outer part of the pallial wall are continued into the

core of the ventricular ridge where they are somewhat more compactly arranged than in the pallium. The section passes through the caudal part of the amygdaloid fissure. It is readily seen that the ventricular ridge corresponds to the external groove and that the fissure is a true fold of the brain wall. Examination of the relations of all parts of the dorsal ridge gives the impression that the ridge is an infolding of the brain wall from this region and that it has pushed forward well toward the rostral end of the hemisphere. Its cell layers come into continuity with those of the pallium here in the amygdaloid fissure and with no other nucleus whatever. They are sharply distinguished from those of the caudate and lenticular nuclei and from the pyriform lobe and are usually separated from these by cell-free zones (figs. 11 to 22). In its rostral part the ridge is sharply separated from all other cell masses and projects freely into the ventricle.

In a transverse section taken at the level of the stria medullaris the cells in this ridge present the arrangement seen in figure 16. All around the ventricular surface are a great number of large and small clusters of cells. Some of these clusters are large, rounded and have a definite outline. Others are very irregular and their outlying cells mingle with the scattered cells between the clusters. The individual cells of the clusters do not differ materially in size from those of the adjacent general pallium but are conspicuously larger than those in any other part of the same section. In the lower part of the ridge, adjacent to the middle ventricular groove, there is a tendency for the cells to be closely aggregated in a large area without special clusters.

The core or central part of the ridge is largely filled by fibers among which are scattered cells. These cells are smaller than those of the clusters. The ventral part of this area is encroached upon by the lentiform nucleus and by the main body of fibers entering or leaving the ridge (figs. 15 to 22). The dorsal part of the central area of the ridge contains a larger number of cells almost evenly scattered. Many of these cells approach in size those of the clusters. This part has almost the appearance of an independent cell-mass and for convenience may be called the

core-nucleus. It extends through nearly the whole length of the ridge as a large, somewhat quadrilateral area bounded laterally by the pyriform lobe and centrally by the cell clusters of the ventricular layer Dorsally it is separated from the thickened border of the general pallium by a cell-free zone of fibers and ventrally it is bounded by the chief fiber mass in the center of the ridge. Toward the rostral end of the ridge this body of cells becomes separated into two masses in the transverse section, owing to the general pallium and lentiform nucleus pressing into it from above and below respectively (fig. 22). Caudally this mass of cells becomes less distinct and merges with the superficial cells of the general cortex as noted at first. Throughout the greater part of its length this core-nucleus is penetrated by numerous fibers which pass up from the internal capsule to the thickened lateral border of the general pallium. Although only a few such fibers are seen in Weigert sections, a great number of non-medullated fibers take this course and they are very conspicuous in Cajal preparations.

Comparison of the turtle brain with that of some lower mammals leads to the suggestion that the dorsal ventricular ridge is the homologue of one of the cell masses which constitute the amygdaloid complex in mammals. This is entirely independent of the homology of the 'epistriatum' with the amygdaloid body suggested by Kappers and others. This ventricular ridge is a wholly different structure from the 'epistriatum' of Kappers. This matter will be discussed in a later paper dealing with the amygdaloid complex in the opossum and some mammals. To follow the comparison here would lead beyond the limits of this paper.

The amygdaloid complex in the turtle includes the following structures: the nucleus of the lateral olfactory tract, the tail of the caudate nucleus, the medial large-celled nucleus and probably the dorsal ventricular ridge. The amygdaloid eminence in the temporal pole is encroached upon by both the hippocampus and the general pallium. The amygdaloid complex has related to it the lateral olfactory tract, a bundle of the medial olfactory tract, the bundle of the diagonal band, the stria medul-

laris, the stria terminalis, fibers of the sensory radiations from the thalamus, an olfacto-hypothalamic projection tract, and an anterior commissure bundle.

The simple enumeration of these tracts shows that while the amygdaloid complex in mammals is a compact collection of cell masses occupying a restricted area in the temporal pole, it is a complex of very diverse elements which have been brought together by mechanical forces and have no primary functional unity.

The extent of the hippocampal formation. The morphological relations of the hippocampal formation have been treated with some fulness in a previous paper ('13 b). There is now to be noticed the boundary between hippocampus and general pallium and the relation of the hippocampal formation to the amygdaloid complex. In the rostral part of the hemisphere the characters shown in figure 47 enable us to fix the boundary of the hippocampus with some degree of accuracy on the basis of cell arrangement. Above the fimbrio-dentate sulcus, which separates the homologue of the fascia dentata from the primordium hippocampi and fimbria, there are first pyramidal cells compactly arranged in a ventricular layer with few peripheral cells. The cells are smaller than the cells in most parts of the general pallium but are neither so small nor so closely crowded as the cells in the deep layers in the middle part of the dorsal pallium in this region. This is the portion which is now generally accepted as the homologue of the fascia dentata of mammals. There is no clear separation or distinction between fascia dentata and hippocampus in this turtle's brain.

Dorsal to this, the cells in the medial wall are less closely arranged, appear larger and are less deeply stained. Many cells here are placed far from the ventricle, even lying in the outer half of the wall. Many cells adjacent to the ventricle are distinctly pyramidal in form and have large, dominating apical dendrites. This loose arrangement of cells rather suddenly gives way to a compact arrangement near the dorso-medial angle of the hemisphere. The dorsal area of compact cells will

be described as part of the general pallium. The area of loose cells probably belongs to the hippocampal formation and the transitional region called the subiculum.

As transverse sections are followed caudad the area which is here assigned to hippocampal formation and subiculum grows rapidly wider. There is nowhere a sharp line of demarcation between hippocampus and general pallium, and none is to be expected. There is everywhere noticeable the point at which the deep cell layer becomes abruptly more compact. This point has been taken as the medial boundary of the general pallium in making the model so that what is there shown as hippocampal formation probably includes the equivalent of the subiculum as well (see fig. 6).

As the sections are traced caudad there is a gradual change in the size of the cells. The cells of the hippocampal formation become smaller, those of the dorsal general pallium somewhat larger, until the difference is at first noticeable, then conspicuous. From the level of the commissures caudad the cells of the hippocampus are much smaller than those of the general cortex.

In the occipital and temporal poles of the hemisphere essentially the same characters are found. Near the fimbria border is an area of dense cells in a deep layer. Next to it is an area with cells loosely arranged and many of them near the periphery (fig. 45). In the temporal region this area of loose cells is narrow and is accompanied by an internal sulcus which serves as an additional landmark. The boundary shown in the model made from transverse sections has been carefully checked up by means of horizontal sections and found to be essentially correct.

The fimbria passes over the interventricular foramen and continues back along the border of the hippocampal formation to which the choroid plexus is attached (fig. 57). The bundle decreases in size as it proceeds but is still fairly large at the caudal end of the choroid fissure. Here the fimbria bends around the end of the fissure and spreads in the medial wall of the ventricle medial to the position of the large-celled amygdaloid nucleus. This is sufficient evidence that the hippocampal formation extends around the end of the choroid fissure into the

medial wall of the temporal pole and confirms the conclusion based on the study of the cells.

In the temporal pole the hippocampus comes into contact with the general pallium and the large-celled amygdaloid nucleus only, not at all with the nucleus of the lateral olfactory tract or any of the small-celled portion of the amygdaloid complex (fig. 8). The hippocampal formation is intimately related in front with the olfactory bulb and secondary olfactory centers. Caudally it forms the border of the pallium adjacent to the choroid fissure and is bounded on the other side by general pallium. There is no continuity of cell masses between the caudal end of the hippocampus and the caudal part of the secondary olfactory centers. The olfactory apparatus taken as a whole does not form a complete ring following the line of junction of the hemisphere with the brain stem ('limbic lobe'). An opening in this supposed ring occurs between the nucleus of the lateral olfactory tract and the hippocampus.

THE GENERAL PALLIUM

The general pallium occupies the dorsal and caudal walls of the hemisphere and reaches well into the temporal pole. Throughout its whole extent it is interposed between the hippocampus on the one hand and the pyriform lobe and nucleus of the lateral olfactory tract on the other. The pyriform lobe and hippocampus meet one another in front of the rostral end of the general pallium near the olfactory peduncle (fig. 7). The general pallium extends forward slightly further than is shown in the model. The presence of a subiculum between the hippocampus and general pallium and of a definite boundary line between the dorsal border of the pyriform lobe and the general pallium has been described above.

Only the most general features in the structure of the pallium can be described in this paper. By far the greater part of the cell bodies are collected in a dense layer near the ventricle. At the dorso-medial border the cells are mostly pyramidal and there are a few cells scattered in the outer part of the pallium. There are many more of the peripheral cells in the adjacent subiculum.

Farther laterally the layer is more compact and the pyramidal form of the cells less evident.

The lateral border of the pallium presents marked characteristics in the rostral half of the hemisphere. In transverse sections the cell layer has a curve near the lateral border which is slight in the caudal part of the hemisphere (fig. 15), becomes more marked rostrally (fig. 17), and near the rostral end is strongly S-shaped (figs. 18, 19). This, together with the slightly larger size of the cells and their arrangement in a very compact layer, suggests rapid growth and mechanical crumpling of the cell layer. This is the border along which internal capsule fibers enter and leave the pallium and there is doubtless a difference of function between this border and the dorsal or medio-dorsal parts of the general pallium. This lateral border becomes gradually thicker as it is followed rostrad and dips down and becomes more and more overlapped by the pyriform lobe. Here the compact plate of cells becomes a thicker mass which in some sections is broken into several masses (figs. 23, 24). At the rostral end this thickened lateral border produces the pallial thickening mentioned in an earlier section.

Toward the rostral end of the pallium the cell layer becomes much less compact except in the lateral thickened border. The pyramidal cells with prominent apical dendrites are mostly confined to the deep layer and outside of these are many cells of stellate or ovoid form. These cells are present in the whole width of the pallium including the subiculum and the lateral thickening. In some sections these cells seem to constitute an incompletely separate layer. When the pallial thickening begins to form a ridge projecting into the ventricle it is noticed that these cells are more numerous in this part of the pallium than elsewhere (figs. 21, 22) and from this point on rostrad they form a conspicuous outer layer of cells in the pallial thickening (figs. 23, 24, 25, 40).

Near its rostral end the total number of cells in the pallium is greatly increased, the deep layer is much thickened and very dense and the outer layer extends well toward the medial border. Indeed, nearly the whole width of the pallium at its rostral end

bears the characteristics of the lateral thick border. In other words, it may be stated that the body recognized in the gross brain as a pallial thickening occupies the rostral end of the general pallial area and extends caudad as a gradually diminishing lateral thick border. The pallial thickening is characterized by the presence of a well-developed peripheral layer of cells and this suggests a special functional significance for this body.

The pallial thickening last described is the most highly specialized part of the general pallium and is farthest removed from the brain stem. The temporal portion of the pallium, adjacent to the amygdaloid fissure, is the most primitive and simple in structure. In the caudal part of the basal surface of the hemisphere, where the temporal and occipital poles may be said to meet, the general pallium presents a somewhat more open arrangement than in most of the pallium (fig. 46). A larger number of cells are placed near the outer surface. From this point rostrad, toward the amygdaloid eminence, there is the line of transition between pallium and hippocampus and an area of pallium in which the cells become more and more irregularly scattered as one follows the sections forward (figs. 45, 44). At its lateral border this pallial area bends inward to become continuous with the cell masses in the dorsal ventricular ridge (figs. 11, 12). As the sections are followed forward it becomes evident that this part of the pallium is related to that basal and caudal part of the ventricular ridge whose ventricular surface is covered by the large-celled nucleus of the amygdaloid complex (fig. 44).

In sections which pass through the caudal part of the pyriform lobe and the deeper and broader part of the amygdaloid fissure (fig. 13), the caudo-lateral prolongation of the nucleus of the lateral olfactory tract appears in the depth of the fissure. Now the general pallial area on the basal surface is bounded by the hippocampus medially and by the nucleus of the lateral olfactory tract laterally. Internally the pallial cells merge with those of the basal lobe of the ventricular ridge. As the sections are followed forward the nucleus of the lateral olfactory tract increases in size while the hippocampal formation disappears from the sections before the tip of the temporal horn of the

ventricle is reached (figs. 45, 44). At the same time the tail of the caudate nucleus appears between the dorsal and basal lobes of the ventricular ridge. The large-celled nucleus now surrounds the temporal horn of the ventricle and occupies the pallial surface medial to the nucleus of the lateral olfactory tract. Now the large bundle of the stria terminalis goes upward and forward from the large-celled nucleus, as above described. Finally the large-celled nucleus disappears from the sections at the level of the stria medullaris.

Thus the general pallium extends forward in the basal wall to the tip of the temporal pole. Its cells in this region are of various forms and are irregularly scattered and there is an intimate merging of the pallium with the large-celled nucleus of the amygdaloid complex. There is no area or avenue of continuity of the cell masses of the pallium with those of the brain stem. There is, however, continuity of the pallium, the large-celled amygdaloid nucleus and the lentiform nucleus of the corpus striatum. The lentiform nucleus imbeds the lateral forebrain bundle and is therefore comparable with the somatic area in the lateral wall of the selachian forebrain. In the turtle there is continuity throughout the cell masses related to the afferent and efferent fibers primarily somatic in function in the lateral bundle, or crus. In the fishes the somatic area is continuous with the sensory centers of the thalamus. That this connection has been lost in the turtle may be attributed to the greater development of the hemisphere which has elongated the crus and drawn the lentiform nucleus away from the thalamus.

The general pallial portion of the hemisphere consists therefore of (1) a broad, rather thin wall forming the roof and caudal pole of the hemisphere; (2) bounding this laterally and anteriorly, a pallial thickening which has a peculiar structure; and (3) a temporal area of simpler structure which is intimately connected with the dorsal ventricular ridge. This ventricular ridge might, indeed, logically be listed as a fourth part of the general pallium.

That these four regions are intimately related and constitute one complex area in the forebrain, comparable to the olfactory

area with its several nuclei, is attested at once by the distribution of the fibers of the cerebral peduncle or internal capsule. This great bundle, where it is about to pass from the brain stem to the hemisphere (fig. 33), is bounded laterally by the optic tract and dorsally by the stria medullaris and stria terminalis. Medial and medio-ventral to this bundle is a large area of fibers which contains (1) the olfactory projection tract of Cajal ('04, fig. 778) descending from the olfactory portion of the amygdaloid complex, and (2) the medial forebrain bundle which follows the crus into the hemisphere and runs forward in relation to the tuberculum, caudate and other olfactory nuclei.

The great lateral forebrain bundle or crus is composed of two parts, dorsal and ventral. The dorsal part is coarse-fibered and well medullated. It comes from the nucleus rotundus and adjacent cell masses in the dorsal part of the thalamus which correspond to the thalamic sensory nuclei in mammals. The ventral part consists of finer fibers which are well medullated at least in their course through the thalamus and corpus striatum. This bundle bends somewhat ventrad and runs caudad on the ventro-lateral surface of the thalamus and mid-brain until some distance behind the third nerve where it becomes more diffuse and seems to end at least in large part before the isthmus is reached. Without going further into descriptive details it is evident that the dorsal bundle contains the sensory radiations from the thalamus to the hemisphere and that the ventral bundle corresponds at least roughly to the efferent tracts from the hemisphere as we know them in mammals.

These two bundles behave differently in the hemisphere. The dorsal deeper bundle bends up rapidly in larger and smaller fascicles through the lateral part of the striatum and enters the core of the dorsal ventricular ridge. The fascicles spread rather wide apart as they pass through the striatum but are all deep beneath the surface of the brain. Upon reaching the ventricular ridge the fibers enter into the formation of a uniform lace-work in the meshes of which the cells of the core-nucleus are evenly scattered. From this lace-work many fibers proceed into the dorsal pallium. This is the appearance seen in Cajal prep-

arations. In Weigert sections the fibers appear to lose their myelin as they enter the dorsal ridge but a small number of medullated fibers are seen running right through the ridge into the pallium (fig. 32). There is at present insufficient evidence to show what proportion of the non-medullated fibers of the sensory bundle reach the pallium but it is clear that a large part of them do so. When transverse sections are followed from behind forward it is seen that the coarse-fibered sensory bundle all rises to the pallium or the ventricular ridge and disappears from the sections before the rostral end of the ridge is reached. The distribution of fibers to the caudal pole of the pallium is partly through the base of the ventricular ridge and partly by way of the fiber-layer of the pallium itself. Very few medullated fibers reach the caudal pole.

The ventral, fine-fibered bundle spreads laterally in the superficial part of the striatum (nucleus lentiformis) and rises toward the lateral border of the pallium. The fascicles, however, slant forward more as they run dorsally and the whole bundle extends much farther forward than the deeper coarse-fibered bundle. The fascicles break up into diffuse fibers before the pallium is reached and many of the fibers may arise from the lentiform nucleus itself. It is clear, however, that the greater part of these fibers enter into the fiber-layer in which the lateral thickened border of the pallial cell-layer is imbedded. Moreover, the greater part of this bundle is related to the pallial thickening.

In sagittal sections (fig. 51) fascicles from the superficial bundle are traced directly up to the pallial thickening through the rostral part of the striatum, and also around the rostral end of the striatum through the cell-free zone between the striatum and the pyriform lobe. It is interesting to note in sagittal sections that medullated fibers enter the pallium and the ventricular ridge only in the rostral part (half or more) of each. The bundles which rise from the crus into the core of the ventricular ridge lose their myelin or disperse so that they can not be traced farther as fascicles.

In Chrysemys marginata the ventricular ridge is smaller than in Cistudo and does not extend as far forward. The pallila

thickening on the other hand is relatively more extensive. In this form the direct course of the superficial fibers of the crus up to the pallial thickening is much more clear than in Cistudo.

It is hoped to test the disposition of these fibers experimentally. If the above conclusions drawn from the study of sections prove to be correct, it is evident that the pallial thickening must be regarded as the chief source of the fibers descending from the pallium to the brain stem. It should be noted that the pallial thickening occupies the same position in the hemisphere as that occupied by the motor area in the lower mammals, except that there is no appreciable frontal association area seen in front of it. Also, the descending fibers lie in front of the sensory radiations as they do in the mammalian internal capsule. It seems probable that the pallial thickening is chiefly motor (efferent) in function and that the ventricular ridge and a large part of the general pallium are sensory and associational. However, it is probable from my present results that the sensory and motor areas are not wholly independent. Also the whole subject of localization within the sensory field is untouched in the present paper.

SUMMARY AND COMMENTS

The advantage offered by the turtle brain for the study of the evolution of the mammalian cerebral hemisphere is that the turtle occupies such an intermediate position between fishes and mammals that it is possible from the standpoint of the turtle brain to recognize the homologous structures in all three groups and to explain the changes which have taken place from the brain of the fish to that of the turtle and from the brain of the turtle to that of the marsupials and mammals. This is due to the fact that among living reptiles the turtles are most nearly related to the ancestors of mammals and still possess a relatively simple and slightly specialized brain. In some points there would be great advantage from the study of the dipnoan brain, to bridge the gap between the fishes and reptiles. This gap is much wider than that between the reptiles and mammals, since neither the specialized fishes nor the amphibians stand in the line of

descent of reptiles and mammals. The dipnoans, or some of them, do stand in this line of descent and the evolution of the brain must be traced from the selachians, through the dipnoans, reptiles and marsupials to the mammals.

The main purpose of the present paper is merely to define the morphological relations of the chief cell masses in the brain of the turtle in order that these may be used in future studies as points of reference in comparing ichthyopsid, reptilian and mammalian brains. This is done in the belief that a satisfactory account of the mammalian and human brain must eventually include an account of the origin and evolution of the several structures together with an explanation of existing structural relationships and the course of their evolution on the basis of environment, habits of life and the function of the several parts.

The olfactory area

Upon comparing the secondary olfactory centers of the hinge turtle with those of fishes, the only very noteworthy fact is the appearance in the turtle of a nucleus of the lateral olfactory tract behind the area occupied by the lateral forebrain bundle. This is a distinctly mammalian character. In the selachian (Johnston '11 a) the lateral forebrain bundle is imbedded in the somatic area in the lateral wall of the slender portion of the forebrain known to many authors until recently as the 'praethalamus,' and the lateral olfactory area lies wholly in front of this. The relations are shown in figure 59, in which are roughly indicated the areas from which alone the pyriform lobe and the nucleus of the lateral olfactory tract may have been developed. In the turtle these areas have moved far backward on the lateral surface and the mass which imbeds the lateral forebrain bundle appears as an island surrounded by olfactory nuclei,—the striatal area surrounded by the pyriform lobe, nucleus of the lateral olfactory tract, the diagonal band, the parolfactory nuclei and the tuberculum. This condition, which is so suggestive of, but not wholly similar to, the mammalian condition, has come about by a spreading and migration caudad of the lateral olfactory area,

chiefly brought about by the great expansion of the dorsal pallium. The expansion of the pallium was accompanied by a great thickening of the lateral bundle and of the cell mass in which it was imbedded. The stretching of the lateral olfactory area accompanying the expansion of the pallium was followed by a collecting together of the olfactory centers into a ring around the striatal area. The striatum then, thickening and bulging outward, came to have its surface freed from the olfactory layer. That a complete ring of olfactory centers was formed around the striatal area was due to the connection which the medial olfactory tract retained with the nucleus of the lateral olfactory tract (fig. 56). This connection of the lateral olfactory nucleus with the medial tract and diagonal band has produced the characteristic bending of a part of the lateral olfactory tract to reach its nucleus in the amygdaloid region (fig. 60).

We have now to note how this condition in the turtle differs from that in the mammal. Although the gross appearance is much the same there is one essential difference, namely, that the striatal area has received a covering of general pallium, converting it into the insula. This has come about by the further expansion of the pallium which has pushed the pyriform lobe down over the striatal area so that in mammals it runs along the ventral border of the insula. Now a part of the lateral olfactory tract sweeps round in a curve to reach its nucleus in the tip of the temporal pole just as in the turtle. There is this difference, however, that the concavity of that sweeping curve is filled not by the striatal area but only by the tuberculum and the anterior perforate space.

The striatal area has thus been the scene of two important migrations of brain substance in the history of vertebrates. Between the fishes and reptiles the olfactory area has spread over the striatum and left its surface free again in the turtle. Between the turtle and mammals the general pallium has spread down over the striatum and left it covered by the insular cortex.

The hippocampal formation

With the expansion of the lateral brain vesicle and the formation of a caudal pole the massive hippocampal primordium in the roof of the selachian forebrain becomes spread out into a thin medial wall of the expanding vesicle. At the same time a part of the choroid roof of the median ventricle is carried out in the medial wall of the lateral ventricle and forms the choroid plexus extending from the interventricular foramen to the temporal pole. The relations of the hippocampus to the secondary olfactory centers in the medial wall have been fully discussed in previous papers and the history of the hippocampus above the reptiles is well known from the work of Elliot Smith and others.

The general pallium

The force which has brought about the changes in the olfactory centers mentioned above is the expansion of the general pallium. This is derived from the anterior end of the somatic sensory column (Johnston '10 c and '11 a) which early in vertebrate evolution extended up into the roof of the forebrain between the lateral olfactory area and the hippocampal primordium. This mass of cells received ascending fibers from the sensory centers in the thalamus and rapidly developed into an important collection of sensory and correlating centers for somatic relations. These centers proved of incomparable value to those vertebrates in which they were the more highly developed, through enabling them to extend the range of environment to which they could adapt themselves.

This expanding general pallium was located between the olfactory area and the hippocampus and was connected with its fellow of the opposite hemisphere by a commissure (corpus callosum) running through the substance of the hippocampus and in close relation to the hippocampal commissure. Under these conditions the expansion of the general pallium brought about great changes in the adjacent structures, as already noted. The first effect was an expansion distinctly in the dorsal or pallial portion of such a lateral forebrain vesicle as exists in the

simpler selachian brains. This tended to produce a caudal pole pushing back over the stem or 'prethalamic' portion. To understand the formation of the caudal pole it is essential to see that the expansion began in this dorsal region and proceeded in the direction eventually assumed by the choroid fissure and the hippocampus. From such a beginning the stretching of the hippocampus and pyriform lobe and the migration of the olfactory area over the striatum all are readily understood. The further expansion of the pallium and the differentiation of special centers in it must be the subject of future work for which the present is preparatory.

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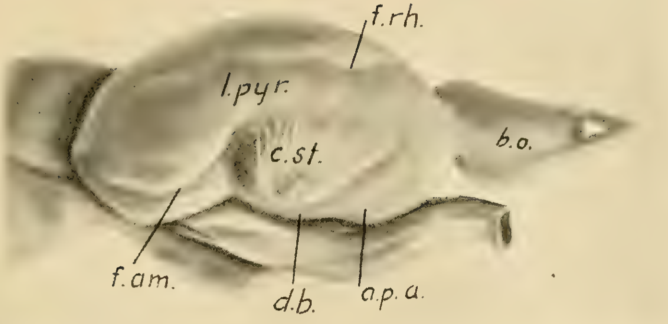
a.p., area parolfactoria
a.p.a., area perforata anterior
b.o., bulbus olfactorius
c.a., commissura anterior
c.h., commissura hippocampi
c.i., capsula interna
ch.op., chiasma opticum
c.post., commissura posterior
c.p.a., commissura pallii anterior
crus, crus cerebri or lateral forebrain bundle
c.st., corpus striatum
d.b., diagonal band of Broca
dec.po., decussatio postoptica
d.v.r., dorsal ventricular ridge
f.am., fissura amygdaloidea
fasc.m., fasciculus marginalis
f.chor., fissura chorioidea
fi., fimbria
f.pc., fasciculus praecommissuralis
f.o., formatio olfactoria
f.p., fissura prima
for.i., foramen interventriculare
f.rh., fissura rhinalis
gl., olfactory glomerulus
g.p., general pallium
gr., granule cells and layer
g.s., gyrus subcallosus
h., hippocampus
hy., hypothalamus
i.C., islands of Calleja
l.pyr., lobus pyriformis
l.t., lamina terminalis
m.fb.bdl., medial forebrain bundle
mi., mitral cells and layer
n.c., nucleus caudatus
n.d.b., nucleus of the diagonal band
n.l., nucleus lentiformis
n.med.a., large-celled medial nucleus of the amygdaloid complex
n.o., nervus olfactorius
n.o.a., nucleus olfactorius anterior
n.p.l., nucleus parolfactorius lateralis
n.p.m., nucleus parolfactorius medialis
n.rot., nucleus rotundus
n.sup., nucleus supraopticus
n.tr.olf.lat., nucleus of the lateral olfactory tract
olf.proj., olfactory projection tract
pa., pallium
pa.th., pallial thickening
p.c., layer of peripheral cells in the pallium
p.h., primordium hippocampi
p.o. pedunculus olfactorius
r.p., recessus praeopticus
r.n., recessus neuroporicus
r.s., recessus superior
s.en., sulcus endorhinalis
s.f-d., sulcus fimbrio-dentatus
s.l., sulcus limitans hippocampi
s.m., stria medullaris
s.p.a., substantia perforata anterior
s.t., stria terminalis
sub., subiculum cornu ammonis
s.v.d., dorsal ventricular sulcus
s.v.m., middle ventricular sulcus
s.v.v., ventral ventricular sulcus
thal., thalamus
t.o., tuberculum olfactorium
t.p., temporal pole
t., tectum mesencephali
tr.d.b., tract of the diagonal band
tr.olf.lat., lateral olfactory tract
tr.olf., tractus olfactorius
tr.olf.med., medial olfactory tract
tr.op., tractus opticus
v.III., third ventricle
v.l., ventriculus lateralis

Fig. 1 Lateral surface of forebrain. Chief features described in text. The fibers in the striatal area are readily seen both in the fresh brain and in brains prepared in bichromate. These fibers are equivalent to the mammalian internal capsule, but the cortical covering of the insula is wanting. The pyriform lobe shows some cross ridges which probably correspond to bundles of internal capsule fibers and thickenings of the lateral border of the pallium. The amygdaloid fissure was especially well developed in this brain. The whole brain never shows the rostral end of the sulcus endorhinalis as well as sections do.



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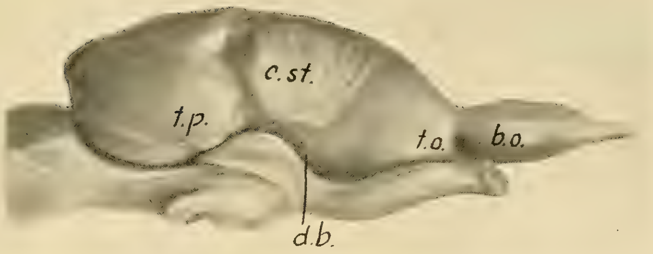

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Fig. 2 A ventral view of the same brain as in figure 1. The diagonal band and the fibers imbedded in it are readily visible in the entire brain, although the fiber-bundles are much more delicate than those of the internal capsule.

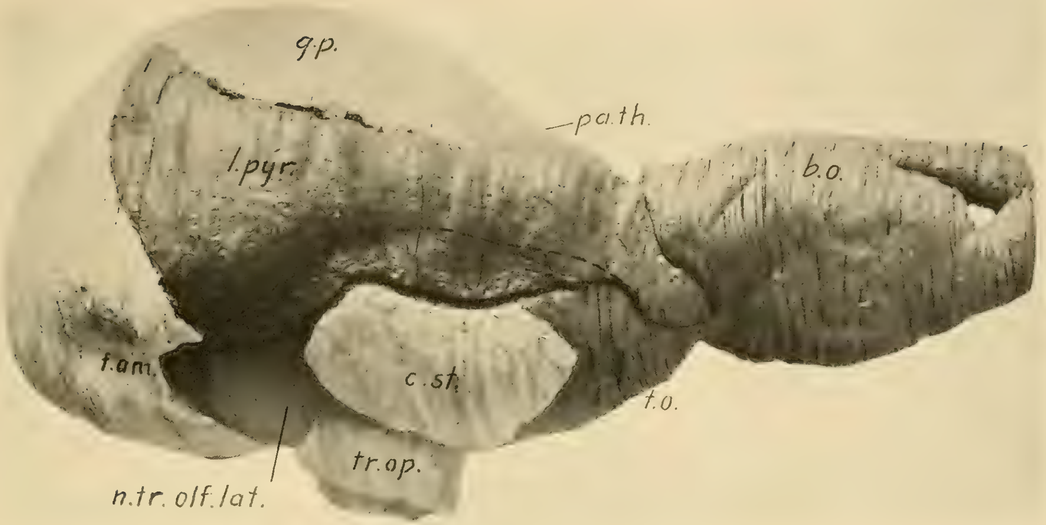
Fig. 3 A medial view of another specimen. (From Johnston '13 b, fig. 20.) The fissura prima curves forward over the parolfactory area. The fimbrio-dentate sulcus runs longitudinally above it. The body between is the primordium hippocampi. Between the fissura prima and the lamina terminalis the diagonal band rises apparently to join the hippocampal primordium directly. The broken line indicates the boundary of the primordium as determined by internal structure. The portion of the diagonal band seen on this surface of the brain is the homologue of the gyrus subcallosus. This figure shows the prominence of the rostral end of the pallium due to the pallial thickening.

Fig. 4 A forebrain from which the entire medial wall of the pallium has been cut away, seen from the medial direction. The large dorsal ventricular ridge is divided into a chief lobe and a basal lobe by a shallow groove. The bifurcation of the middle ventricular groove is not well shown. One branch descends into the temporal horn of the ventricle; the other runs for a short distance in the bottom of the shallow groove on the dorsal ridge. Compare figure 10. This brain shows an unusual prolongation of the basal part of the dorsal ridge into the caudal pole. The part of the striatum seen here is the head and tail of the caudate nucleus.

Figs. 5 to 10 These are photographs of a model of the right half of the forebrain made by the method of plate reconstruction. The method of building up and dissecting the model is explained in the text. Before photographing, the outer surface of the model was lightly smoothed and then painted in two colors. All the olfactory centers including the hippocampus were painted a light yellow-green. The somatic structures, striatum and general pallium, were painted light blue. In the photographs all the olfactory centers have a dark tone. The ventricular surfaces and the cut surfaces have received no treatment whatever. The hypothalmic region was not completed.

Fig. 5 Lateral surface of the model. The dorsal border of the pyriform lobe is sharply marked through its whole length. The caudal border is only arbitrarily fixed. A broken line marks the limit between the large-celled and small-celled parts of the pyriform lobe. The olfactory part of the amygdaloid eminence appears depressed owing to its color and to its being in shadow. Compare figure 8. The structures surrounding the striatal area constitute a continuous ring of small-celled olfactory nuclei.

Fig. 6 Medial view of the model. The lip of the choroid fissure and the lamina terminalis are painted white. The model is cut between the hippocampal commissure and the anterior commissure, so that the commissure may be removed with the whole hippocampal formation. A broken line indicates roughly the boundary between the hippocampus proper and the subiculum. Probably too large an area is included in the subiculum at the anterior end. The somatic pallium should have been carried farther forward here in constructing the model. Note the oblique position of the peduncular constriction. Note also the fissura prima, the fimbrio-dentate sulcus and the moulding of the caudal pole around the thalamus and midbrain.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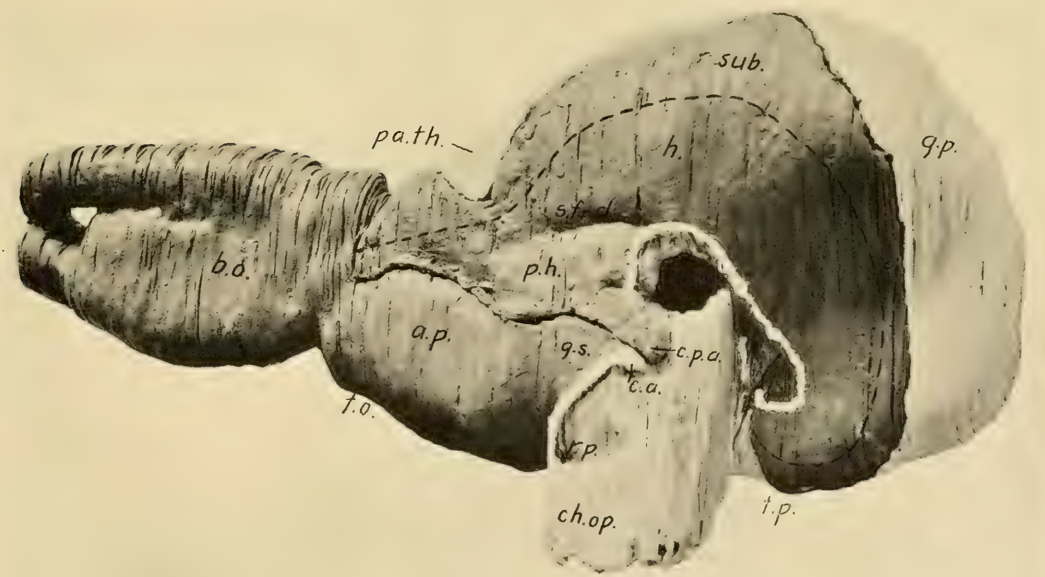
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Fig. 7 Dorsal view of the model. This requires no comment except to point out that the general pallium should have been continued somewhat farther forward at the expense of the subiculum cornu ammonis.

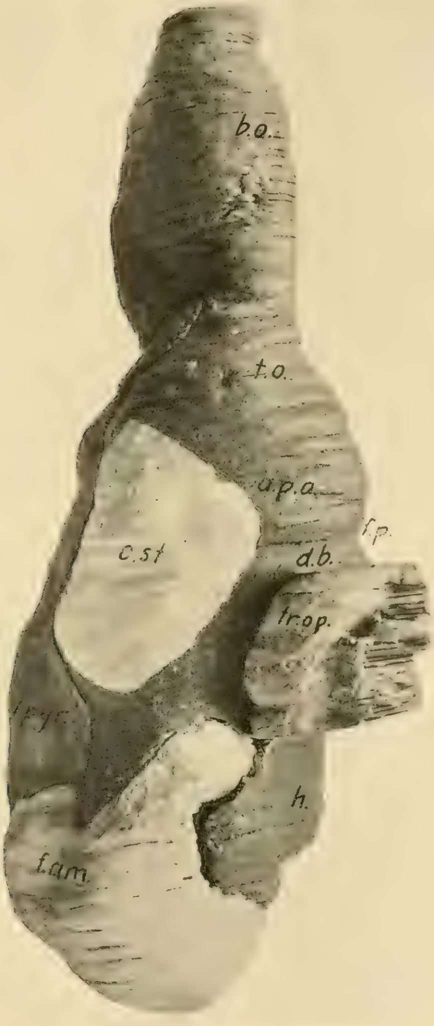

Fig. 8 Ventral view of the model. This view shows well how the striatal area is completely surrounded by olfactory centers. It also shows that the general pallium extends into the amygdaloid prominence of the temporal pole so as to intervene between the hippocampus and the secondary olfactory nuclei. The temporal pole of the hippocampal formation has no direct relation with the secondary olfactory nuclei on the basal aspect of the brain.

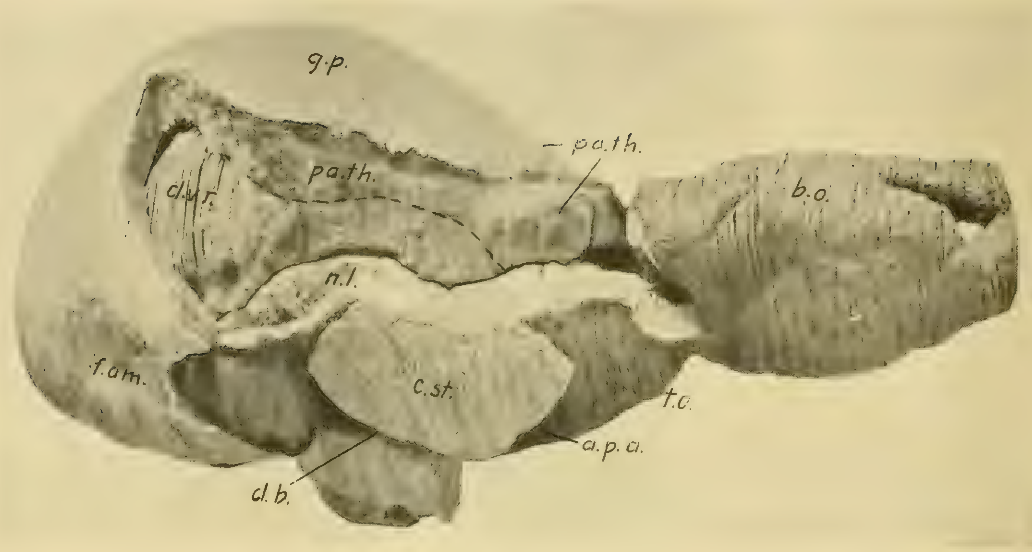

Fig. 9 Lateral view of the model with the pyriform lobe removed. At both its rostral and caudal ends the pyriform lobe forms the whole thickness of the wall over small areas, so that the ventricle is opened in this photograph. Through the greater part of its length the pyriform lobe overlies the thickened lateral border of the pallium and the dorsal ventricular ridge. A broken line marks the boundary between the pallium and this ridge. Along this line a cell-free zone separates the pallium from the ridge but the two can not be dissected apart owing to the continuity of their cell masses in the region of the amygdaloid fissure. The thickening of the lateral border of the pallium which causes the bulging out of the pyriform lobe near its rostral end is clearly seen in this photograph.

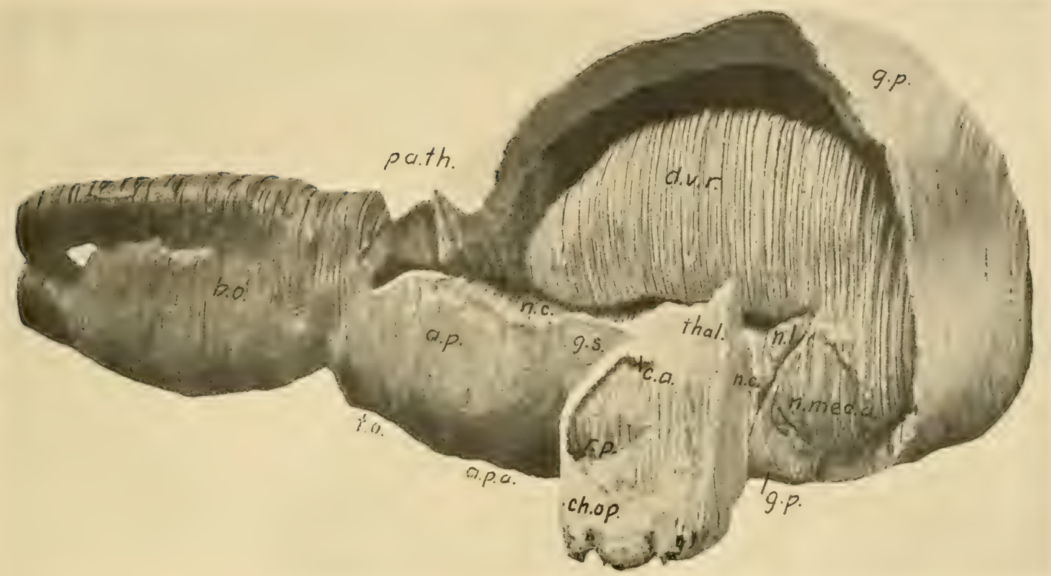

Fig. 10 Medial view of the model with the hippocampus removed. The pallial thickening is perhaps better seen here than in the dissected brain (fig. 4). That part of the thalamus which appears behind the anterior commissure is continuous laterally with the tail of the caudate. The ventricular ridge and general pallium are separated from the striatum by a cut which follows the middle ventricular groove to the end of its dorsal branch, and by a cut which runs diagonally downward and forward from the end of the first one and disappears behind the hypothalamus in this view. The bifurcation of the middle ventricular groove is seen just behind the upper angle of the thalamus. From this point the temporal branch descends into the temporal horn of the ventricle. Its course forms a letter X with the second cut above described. Following the course of this groove is the small ridge described in the text as imbedding part of the stria terminalis related to the basal lobe of the ventricular ridge. From this ridge the bundle goes forward in the caudate. The tail of the caudate barely appears in this figure behind the thalamus (n. c.) and bounded by the temporal branch of the middle groove. The thickening and fusion of the caudate with the nucleus of the lateral olfactory tract in the amygdaloid complex lies just lateral to this point. It is in this region that a great hypertrophy of the common caudate-amygdaloid mass produces the 'epistriatum' in the lizards. The triangular area between the two cuts above described belongs to the lentiform nucleus. Note that the general pallium is continuous with the lentiform nucleus through the basal lobe of the ventricular ridge (medial nucleus of amygdaloid complex).

Figs. 11 to 30 Transverse sections of the right hemisphere drawn from sections stained to demonstrate the size and grouping of the cell bodies. The contrasts and lines of separation are not exaggerated. Magnification, 17.5 diameters. The position of each of these sections is indicated in figure 58.

Fig. 11 Section through the base of the dorsal ridge. The dense layer in the medial wall of the pallium is in part hippocampus. The rest of the section belongs to general pallium, with which the ridge is in connection.

Fig. 12 Section a short distance behind the choroid fissure. The dense pallium in the medial wall is hippocampal. The dorsal ridge appears as an infolding of the general pallium. The pyriform lobe presents a confused arrangement of its cells.

Fig. 13 Section at the caudal border of the choroid fissure and the base of the amygdaloid fissure. Hippocampal formation appears both above and below the choroid fissure. The large-celled nucleus appears on the ventricular surface of the basal lobe of the great ventricular ridge. The nucleus of the lateral olfactory tract appears near the base of the amygdaloid fissure. Between them the general pallium is continuous with the central core of the ventricular ridge. Note the small ridge below, which contains the stria terminalis bundle. From this level forward the subiculum cornu ammonis is a conspicuous feature.

Fig. 14 Section through the extreme rostral end of the temporal horn of the ventricle. Hippocampal formation has disappeared below the choroid fissure. The large-celled nucleus surrounds this part of the ventricle. The nucleus of the lateral olfactory tract has grown larger and the caudate nucleus appears and is fused with it. The nucleus lentiformis begins to take shape.


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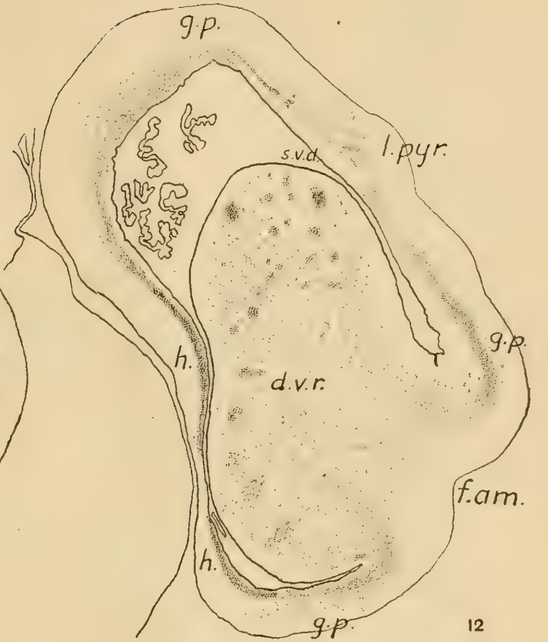
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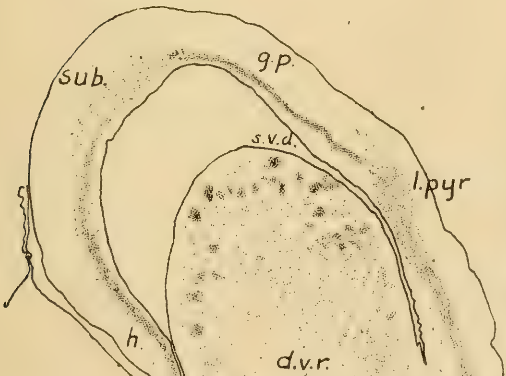
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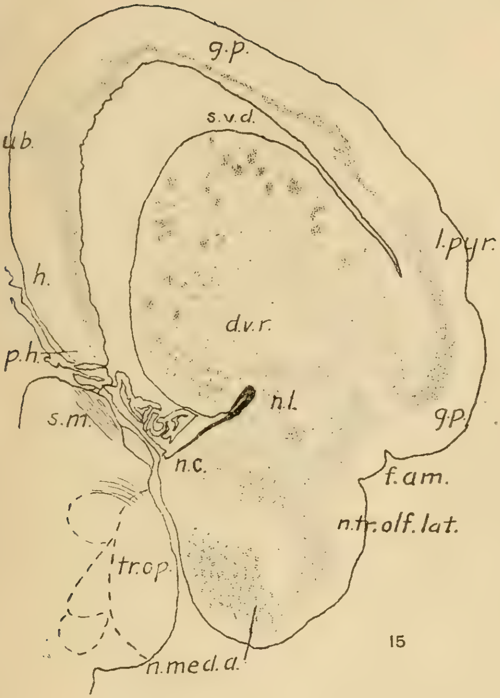
Fig. 15 Section at the base of the amygdaloid fissure. The general pallium still makes connection with the ventricular ridge and intervenes between the pyriform lobe and the nucleus of the lateral olfactory tract. This last is now larger and merges broadly with the caudate. The lentiform nucleus shows some dense collections of cells.

Fig. 16 Section through the stria medullaris. This is about the largest and densest part of the small-celled area of the amygdaloid complex, consisting of the caudate and nucleus of the lateral olfactory tract. The great enlargement of this body produces the 'epistriatum' in lizards. The olfactory projection tract and part of the stria terminalis are related to this (compare fig. 49) while the stria medullaris enters the neuropile surrounding the rostral end of the medial nucleus. Note the rapid thickening of the lateral border of the dorsal pallium in figures 15 and 16. An angle of the general pallium connected with the ventricular ridge still intervenes between the pyriform lobe and the nucleus of the lateral olfactory tract.

Fig. 17 Section through the extreme tip of the temporal pole or amygdaloid prominence and through the caudal part of the junction of thalamus and striatum. The nucleus lentiformis is larger and the nucleus of the lateral olfactory tract appears divided. The upper portion will in the next figure join the pyriform lobe. The core-nucleus of the ventricular ridge is now well defined. Note the olfactory projection tract curving over the crus.

Fig. 18 Section through the commissures just rostral to the inter-ventricular foramen. The crus bends laterad into the lentiform nucleus. It separates the caudate from the nucleus of the diagonal band which is a continuation of the nucleus of the lateral olfactory tract. Note the continuity of the caudate with the nucleus anterior region of the thalamus in figures 17 and 18. Note also the rapid enlargement of the primordium hippocampi in these figures as it approaches the level of the commissure. For the disposition of the commissures compare figures 32, 48 and 52.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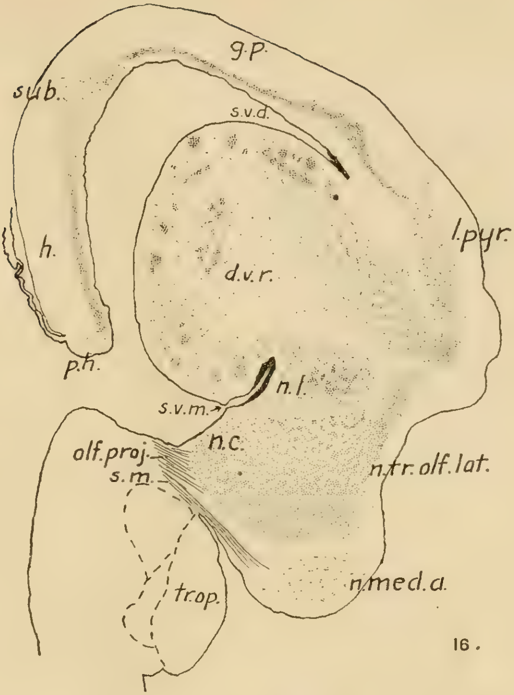
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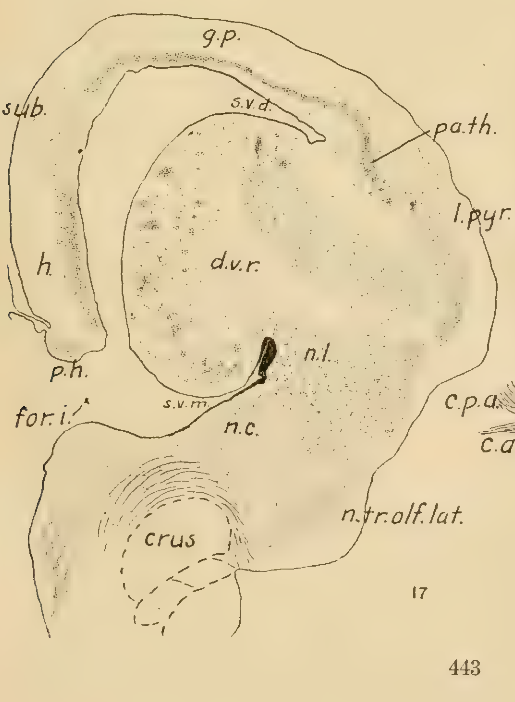
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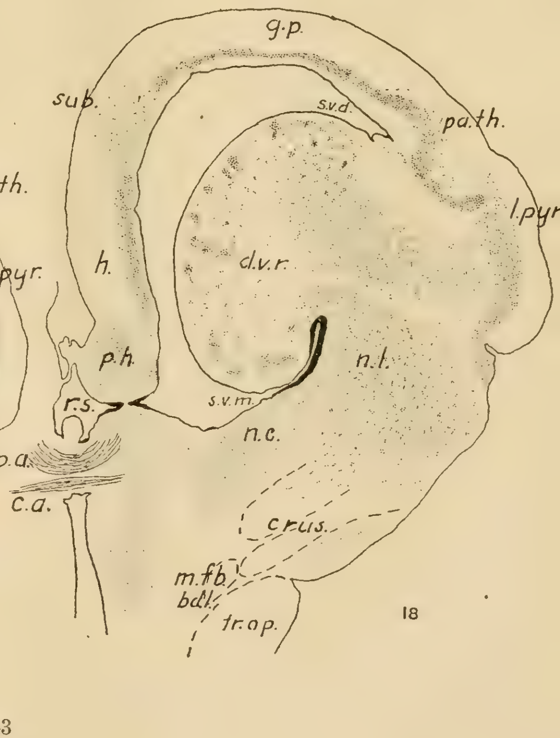
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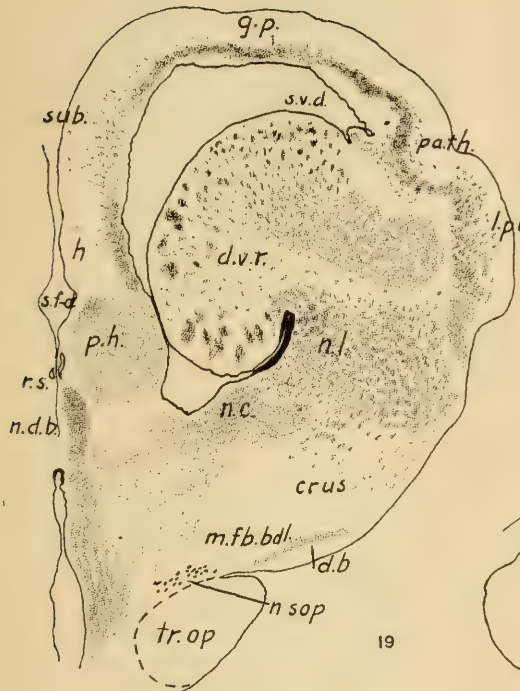
Fig. 19 Section in front of the commissures and behind the optic chiasma. The lentiform nucleus is large; the crus occupies the clear space below it and sends fascicles up through it (internal capsule). The nucleus of the diagonal band forms a thin cell layer between the fiber layer of that band and the medial forebrain bundle. The caudate is small. The upper end of the nucleus of the diagonal band appears here in the gyrus subcallosus adjacent to the hippocampal primordium and the recessus superior. Note the distinct large- and small-celled portions of the pyriform lobe. Also the general increase in thickness and more open formation of the cell layer of the dorsal pallium.

Fig. 20 Section through the optic chiasma. The ventricular ridge grows smaller and the definite pallial thickening begins. The hippocampus proper grows narrow. The hippocampal primordium is only apparently fused with the parolfactory nuclei, as explained in the previous paper. The diagonal band and its nucleus move to the angle between the basal and medial walls. The sulcus endorhinalis separates the small-celled from the large-celled part of the pyriform lobe. The lentiform nucleus is quite superficial in this and several following figures. The clear zones above and below the core-nucleus of the ventricular ridge and between that and the pyriform lobe are the spaces through which internal capsule fibers run to the ridge and the general pallium.

Fig. 21 Section at the level of the gyrus subcallosus. The changes noted in the last section have been carried farther. The lentiform nucleus shows rows of cells due to the arrangement of bundles of internal capsule. In this and figure 22 the diagonal band nucleus merges with the superficial layer of the anterior perforate space and tuberculum olfactorium.

Fig. 22 Section through the anterior end of the dorsal ventricular ridge. The core-nucleus is here divided into two areas by pressure from the pallial thickening. This thickening is the most conspicuous feature of the section. Note the development of a layer of peripheral cells in figures 20, 21 and 22. Compare figure 40. The caudate begins to enlarge and the lentiform to decrease.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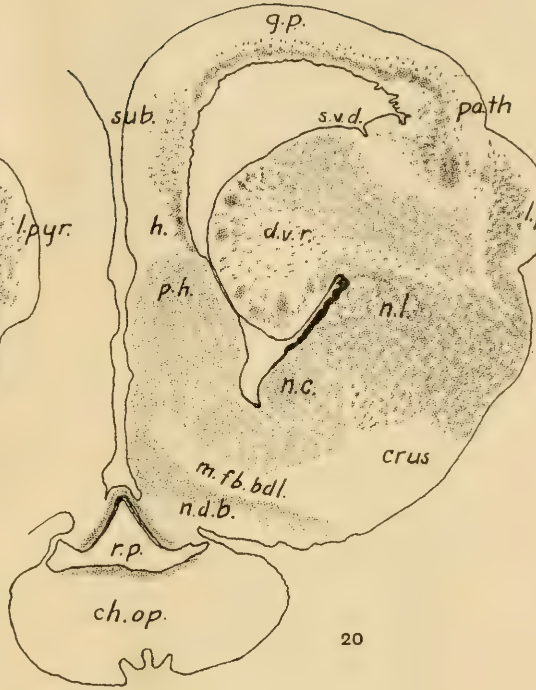
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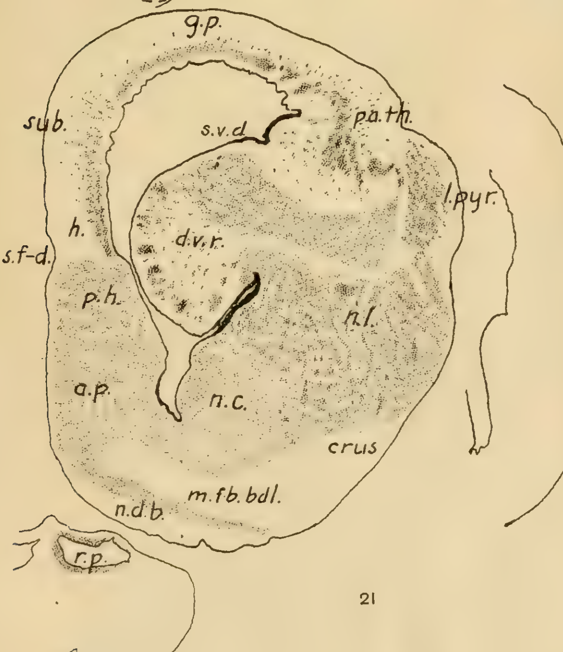
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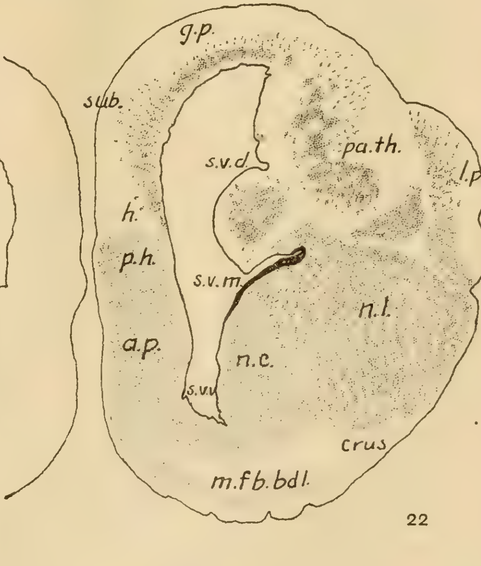
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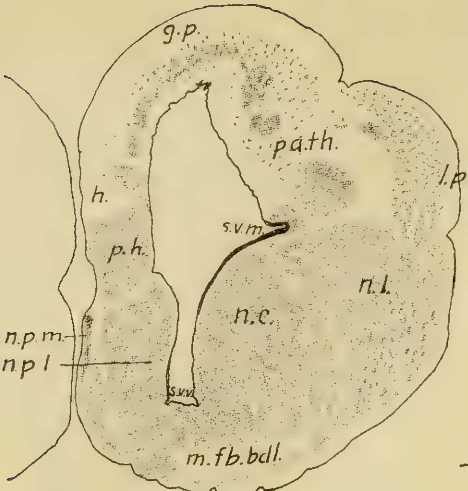

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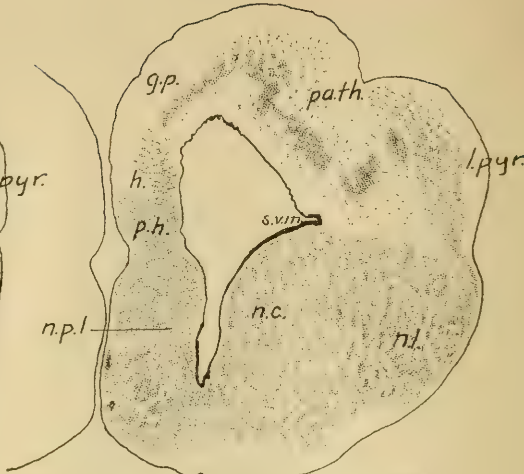

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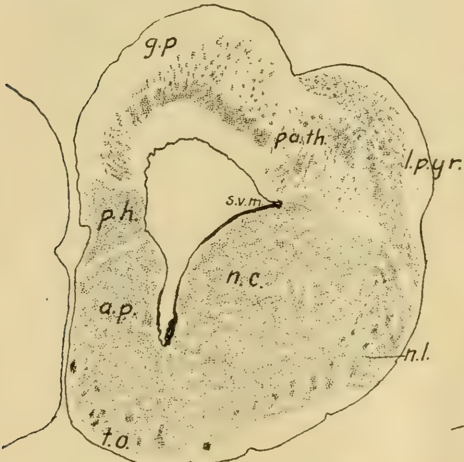

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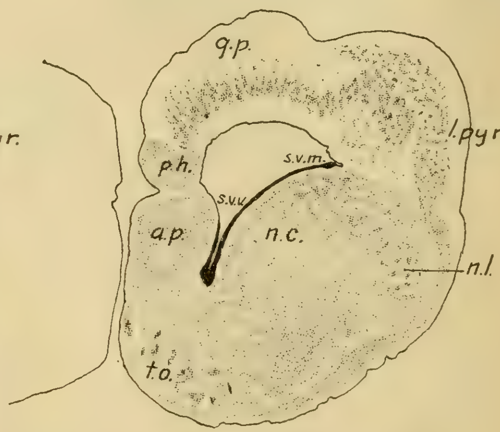

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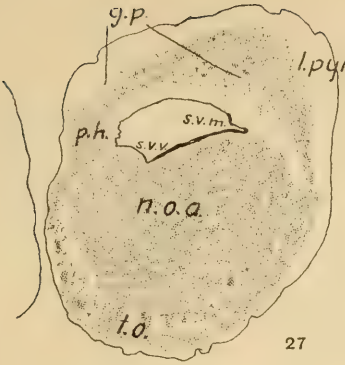
Fig. 23 Section through the pallial thickening in front of the ventricular ridge. In this and the next three figures the pyriform lobe is bulged out by the pallial thickening. Although the lentiform nucleus still meets the ventricle, the caudate is greatly enlarged. From here forward the hippocampus is scarcely if at all recognizable. The subiculum continues between the general pallium and the hippocampal primordium. The dividing line between primordium hippocampi and parolfactory area is again clear. In this section the ventral ventricular groove reaches its greatest depth and width. Forward from this the thickening of caudate, parolfactory nucleus and tuberculum nearly obliterate it.

Fig. 24 Section through the middle of the pallial thickening. Islands of Calleja begin to appear in the medial wall. The lentiform nucleus is pushed toward the surface by the caudate. For a detail of the pyriform lobe and part of the pallial thickening compare figure 40.

Fig. 25 Section through the caudal part of the tuberculum olfactorium and the head of the caudate. Note the high dorsal prominence caused by the pallial thickening. This scarcely shows satisfactorily in the figures of the whole brain or model. A part of the apparent thickness of the cell layer is due to the section being slightly oblique to the curvature of the dorsal pallium but the appearance of a distinct peripheral layer of cells is not due to this. Islands of Calleja are grouped in the medio-basal angle. Dark masses farther laterad are merely clumps of large cells in the lentiform nucleus.



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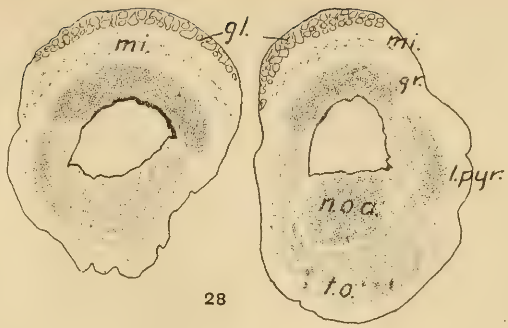

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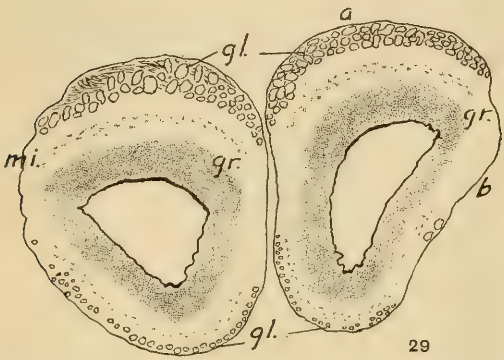

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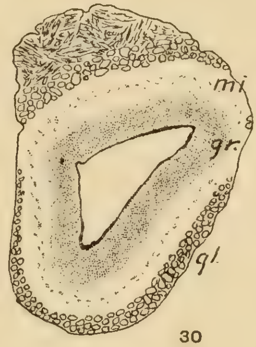

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Fig. 26 Section a short distance in front of the last. It shows the rostral end of the lentiform nucleus and the spreading of the small-celled part of the pyriform lobe over the striatum as the superficial layer of the tuberculum. The whole width of pallium in figs. 25, 26 has the characters of the thickening.

Fig. 27 Section through the rostral part of the tuberculum. The section passes just behind the peduncular constriction dorsally. Olfactory formation begins to appear 225 microns farther forward. The head of the caudate together with the deep or lateral parolfactory nucleus form one rounded mass covered externally by tuberculum. This is the nucleus olfactorius anterior of authors. Islands of Calleja are in the deep layer of the tuberculum. The tuberculum is continuous with the medial parolfactory nucleus and with the pyriform lobe. The pyriform lobe spreads medially in dorsal wall. General pallium is still present toward medial border and in some clusters of cells beneath pyriform lobe.

Fig. 28 Section through the olfactory peduncle. Both sides are shown, the left side being sectioned near the rostral end of the oblique peduncle, the right side near the caudal end of the peduncle. On the right side fully developed olfactory formation appears in the roof; in the lateral wall the pyriform lobe; below, the end of the nucleus olfactorius anterior and the tuberculum.

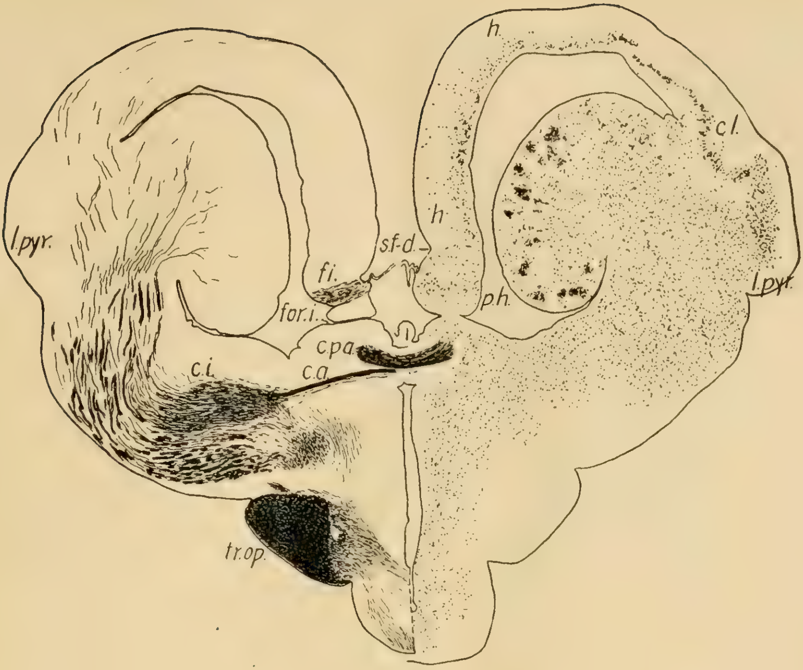
Fig. 29 Section through the caudal part of the olfactory bulb. Note the elliptical form of section on the right, the greater number of cells where olfactory glomeruli are present and the distribution of mitral cells with reference to the glomeruli. *a*, *b*, regions of this section which are drawn in figure 31.

Fig. 30 Section through the anterior part of the right bulb. Note the triangular form of section and the fact that the dorsal root of the olfactory nerve is just entering the bulb. The bulb is nearly surrounded by glomeruli and the mitral cell layer is continuous except for a short space on the lateral surface where glomeruli are absent.

Fig. 31 Two portions from the section drawn in figure 29 to show the modification of the structure of the olfactory formation due to the presence of glomeruli. The part of the section drawn in *a* and *b* respectively is indicated by the same letter in figure 29. Where glomeruli are present the granule cell layer is considerably thicker and more dense and the layer of large mitral cells is added. Magnification 110 diameters.

Fig. 32 Transverse section at the level of the commissures. From Johnston '13b, fig. 17. The right side of the drawing was taken from a section adjacent to that from which figure 18 of the present paper was drawn. The left side was drawn from a Weigert series. The crus shows the two chief bundles described in the text. To what extent the fascicles of the two bundles intermingle as they are distributed to the pallium and the ventricular lobe it is impossible to say from sections of normal brains. The relation of the anterior commissure to the internal capsule is better shown in figure 48. Medial to the crus appear two other bundles. The darker one is the medial forebrain bundle, the lighter is the olfactory projection tract.

Fig. 33 A section similar to the last, taken at the level of the stria medullaris. From Johnston '13b, fig. 18. The two bundles of the crus are separated by a notch medially. The medial forebrain bundle is ventral to the olfactory projection tract and in contact with the postoptic decussation. The lower part of the fiber area beneath the letters *c.i.*, belongs to the olfactory projection tract. The stria medullaris is more superficial.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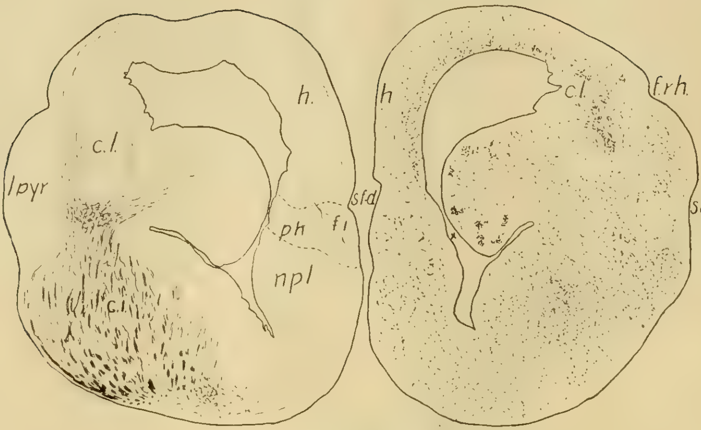

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Fig. 34 A section similar to the last, taken near the rostral end of the ventricular ridge. The internal capsule fibers are related largely to the pallial thickening (c.l.). The medial part of the fiber bundles below belongs to the medial forebrain bundle. Its fibers are related only to the caudate and olfactory nuclei.

Fig. 35 Vesicular structures in the caudate nucleus. *a*, outline of a transverse section to indicate the position in which such vesicles are found. This is nearly at the same level as figure 25. Vesicles are found both rostral and caudal to this level. *b*, an oblique section of a vesicle the lumen of which contains a flattened nucleus of unknown character. Two blood corpuscles are seen. Vesicles often have capillaries closely connected with them. *c*, a transverse section of a vesicle with very sharply defined lumen. Note the granular contents of the inner ends of the cells. There are also faintly stained granules in the lumen. The isolated nuclei in *b* and *c* are nuclei of nerve cells lying near the vesicles. Magnification in *b* and *c*, 625 diameters.

Fig. 36 Section of the thickened ependyma surrounding the middle ventricular groove including a part of the lentiform nucleus. The nerve cells are drawn in outlines, the nuclei of the ependyma cells in black. The lines represent the peripheral processes of the ependyma cells. From the same section as figure 16. Magnification 112 diameters.

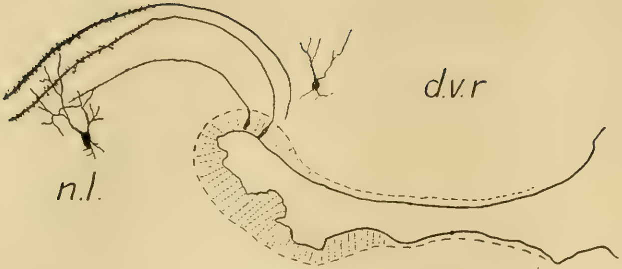

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Fig. 37 Same region as figure 36 but on the left side of the brain. A drawing from a Golgi section to show the ependyma cells in the dorsal lip of the middle ventricular groove, and their curved processes.

Fig. 38 Transverse section through the tuberculum olfactorium to show the grouping of cells in the islands of Calleja. From a section adjacent to that shown in figure 24. Magnification 110 diameters. The medio-basal angle of the left side and a small part of that of the right side are included. *a, b, c, d*, typical islands. *e*, an island in which larger and small cells are mingled. In some islands similar to this the small cells definitely show the vesicular arrangement with lumina. *f*, a vesicle similar to those shown in figure 35. Only the nuclei are drawn.

Fig. 39 Transverse section through the upper end of the gyrus subcallosus, showing the dense nucleus of the diagonal band close to the recessus superior. From the same section as figure 19. The position of the hippocampal commissure shows that this nucleus pushes up near the medial surface above the level of the commissure. This is shown in the model, but the ventral border of the hippocampal primordium in front of the commissure curves dorsally still more than is shown in the model (fig. 6). Note how much smaller these cells are than those of the adjacent hippocampal primordium. Indeed these are among the smallest cells in the forebrain. Magnification 110 diameters.

Fig. 40 Transverse section through the pyriform lobe and the pallial thickening to show the form and grouping of the cells. From the same section as figure 24. Magnification 70 diameters. In the upper part of the figure enough of the pallium is drawn to show the importance of the peripheral layer of cells. The deeper cells are smaller and so closely crowded that their processes seldom show at this magnification. The thick dendrites of the larger cells in the pyriform lobe, however, are clearly seen. It is evident that the large cell clusters belong to the pallium and not to the pyriform lobe.

Fig. 41 Transverse section of the caudal part of the pyriform lobe. From the same section as figure 13. Magnification 70 diameters. In the upper part of the figure is seen the sharp dividing line between pyriform lobe and general pallium. No well-marked line of division is seen below.

Figs. 42 to 45 Four transverse sections through the region of the medial nucleus of the amygdaloid complex. From the same sections as 16, 15, 14, 13 respectively. Magnification 70 diameters.

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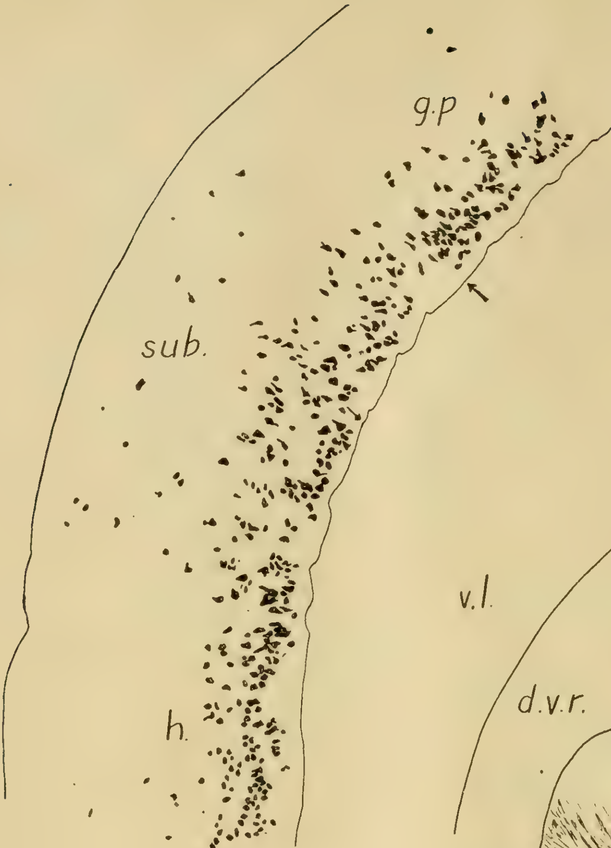
Fig. 42 In this is seen the common mass of small cells formed by the caudate and the nucleus of the lateral olfactory tract. Below it is a mass of neuropile in which appear a considerable number of larger cells belonging to the medial nucleus. The stria medullaris enters into this neuropile while the olfactory projection tract and stria terminalis in part are related to the small-celled nucleus (compare fig. 49).

Fig. 43 Only a little of the small-celled mass is shown. The medial nucleus is larger and more dense and has shifted toward the medial wall.

Fig. 44 The medial nucleus is still larger and surrounds the temporal horn of the ventricle, the rostral end of which is cut by the section. Immediately caudal to this the medial wall of the ventricle is occupied by hippocampal formation.

Fig. 45 In this section the medial nucleus occupies the ventricular surface of the basal lobe of the great ventricular ridge. Ventrally this mass of cells merges with the general pallium. The dense lamina in the medial wall belongs wholly or in part to the hippocampal formation. The small ridge in the lower angle of the ventricle lodges part of the stria terminalis bundle which spreads over the ventricular surface of the medial nucleus.

Fig. 46 Transverse section through the base of the ventricular ridge near its caudal end. From the same section as figure 11. Magnification 70 diameters. The relations are described in the text. The figure shows typical pallial walls laterally and ventrally which appear to be involuted to form the ventricular ridge.



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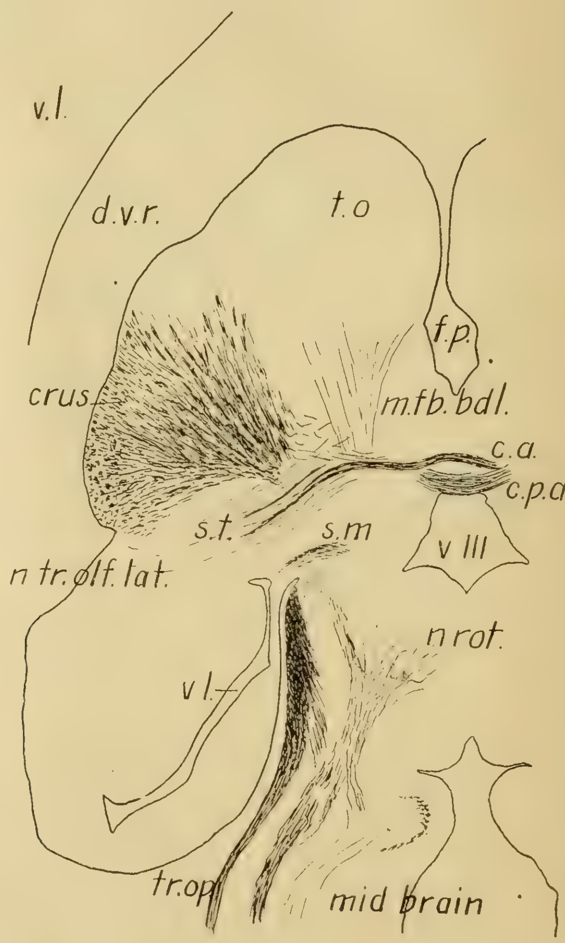

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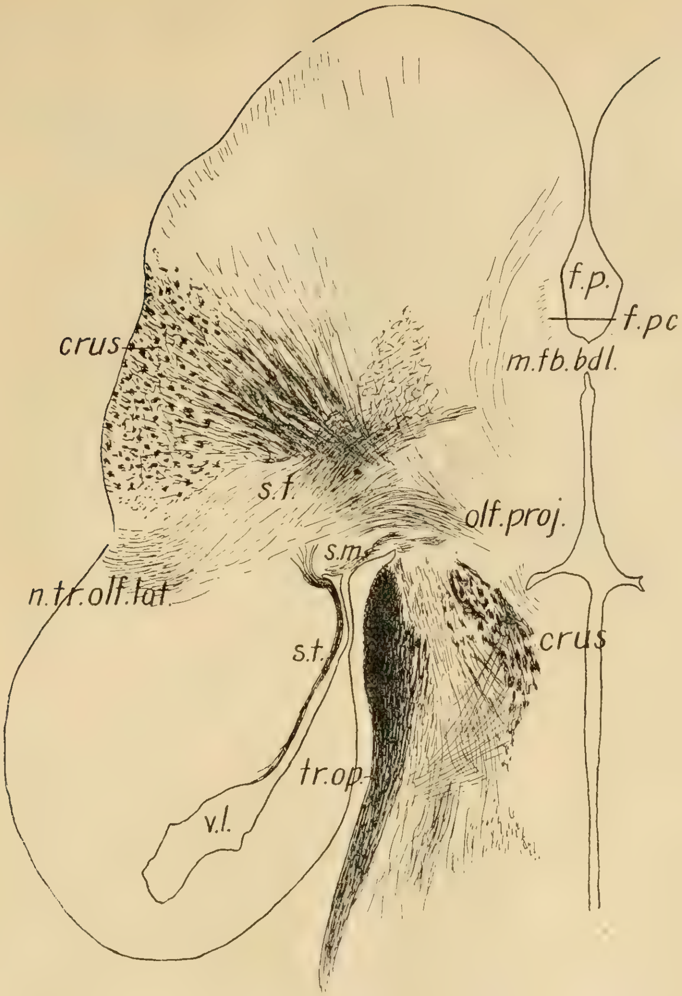

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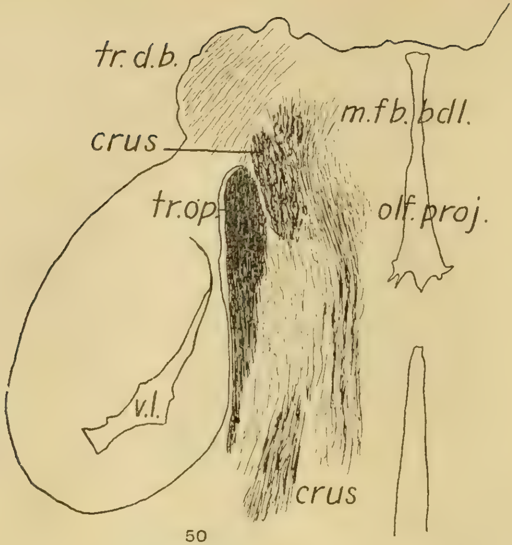
Fig. 47 A drawing of the subiculum region from the same section as figure 17. Magnification 70 diameters. The figure shows very inadequately the relatively dense layer of the hippocampus below, the more open arrangement of the cells in the subiculum and the abrupt medial border of the general pallium above. This border is marked by the arrow.

Fig. 48 Horizontal section from a Weigert series to show the anterior commissure and stria terminalis. The section is taken just at the level of the most dorsal part of the stria terminalis where it curves over the internal capsule. At this point the anterior commissure meets the stria (compare fig. 32) and continues with it into the small-celled nucleus of the amygdaloid complex.

Fig. 49 Horizontal section somewhat ventral to the level of that drawn in figure 48. This is from another series. The section passes through the lower or ventral part of the stria terminalis where it lies close upon and a little intermingled with the internal capsule. The section is drawn to show that the stria terminalis and the olfactory projection tract are divisions of a common broad bundle arising from the small-celled part of the amygdaloid complex. The bundle which enters the stria terminalis from the basal lobe of the ventricular ridge is drawn although it is almost wholly non-medullated. It can not be traced farther forward in these sections.



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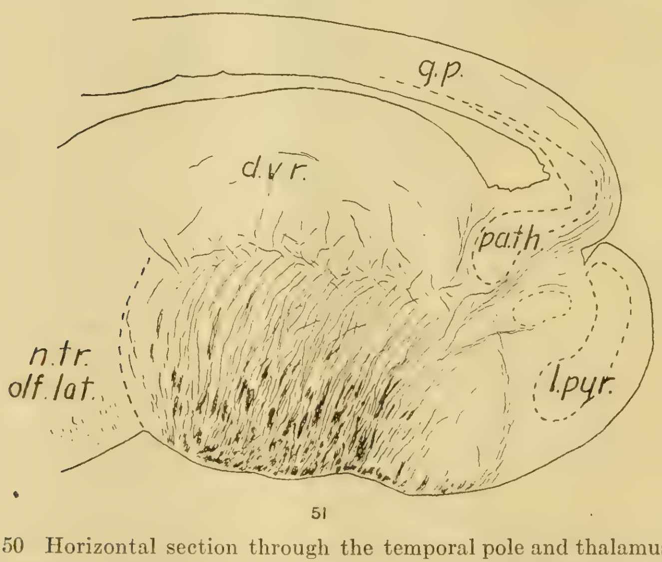

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Fig. 50 Horizontal section through the temporal pole and thalamus. Same series as figure 49. This section shows the fiber bundle of the diagonal band where it crosses the basal surface of the crus and medial forebrain bundle.

Fig. 51 Parasagittal section close to the right lateral surface. Weigert stain. The cell masses of the pyriform lobe and pallial thickening are outlined in broken lines; also the line of division between the striatum and the amygdaloid complex. The figure shows especially the fibers of the internal capsule entering the pallial thickening.

Fig. 52 Section from the same series as the last. Near the median plane. The section shows the hippocampal commissure rising in the hippocampal primordium to join the fimbria system. There are shown also the relations of the sensory bundle of the crus, the olfactory projection tract and the medial forebrain bundle.

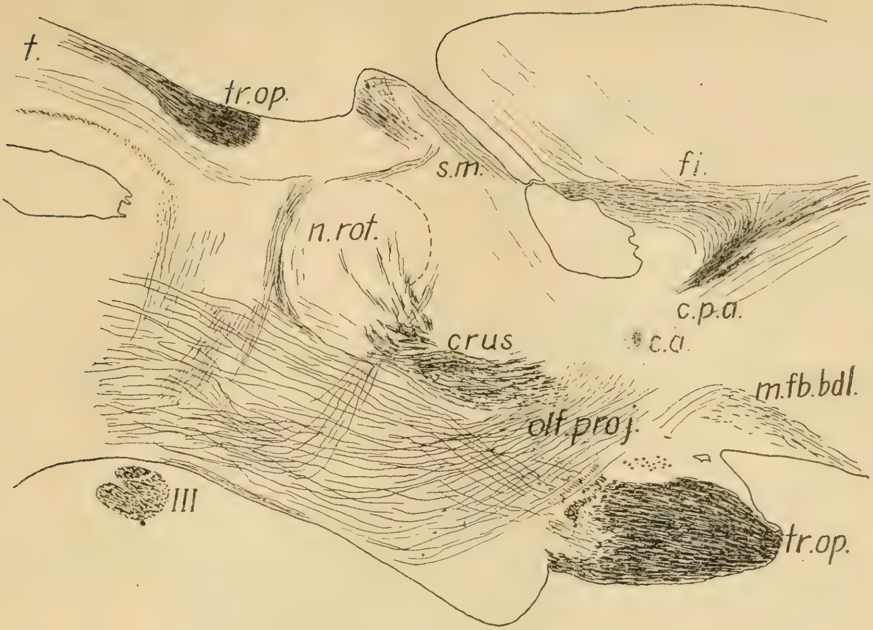

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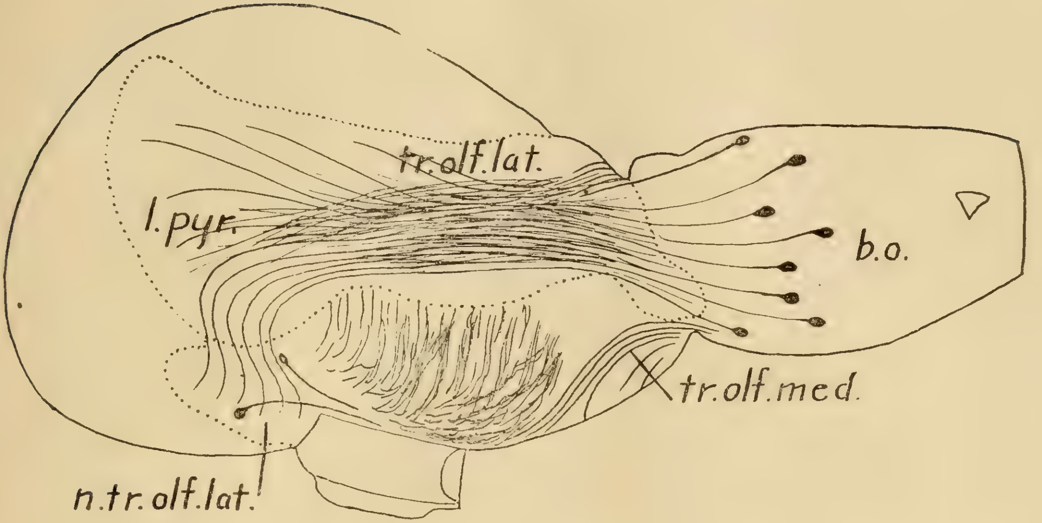
Fig. 53 A section from the same series as the last. It is taken from the left side of the brain. Owing to the oblique plane of the sections this is near the median plane at the level of the third nerve, but farther from the middle in the forebrain than in figure 52.

Fig. 54 A section from the same series, farther laterad than the last. This section shows a part of the sensory and the motor bundle of the crus, the olfactory projection tract and the median forebrain bundle. It is especially interesting to note from these sections that both the olfactory projection tract and the median forebrain bundle run almost wholly to the tegmental region or farther caudad, whereas it has been supposed that they both end for the most part in the hypothalamus.

Fig. 55 A diagram of the lateral olfactory tract together with a part of the medial olfactory tract and of the bundle of the diagonal band. Outline taken from figure 5. The figure shows the bundle which bends down behind the striatal area to end in the nucleus of the lateral olfactory tract in the amygdaloid eminence. At *a* is seen the bundle which comes from the medial wall of the olfactory bulb, crosses over the dorsal surface in the peduncular groove and joins the lateral tract. The whole course of the diagonal band can not be seen in this lateral view.

Fig. 56 A diagram of the olfactory tract in ventral view. Outline taken from figure 8. The medial and lateral bundles of the olfactory tract are separated by the striatal area containing the fibers of the crus. A bundle of the lateral tract curves around lateral and caudal to this area to reach the nucleus of the lateral olfactory tract, while a bundle of the medial tract passes along the ventral border of the striatal area to reach the same nucleus. From this nucleus, then, fibers enter the stria medullaris and the bundle of the diagonal band. The latter go to the hippocampus by way of the precommissural fornix system.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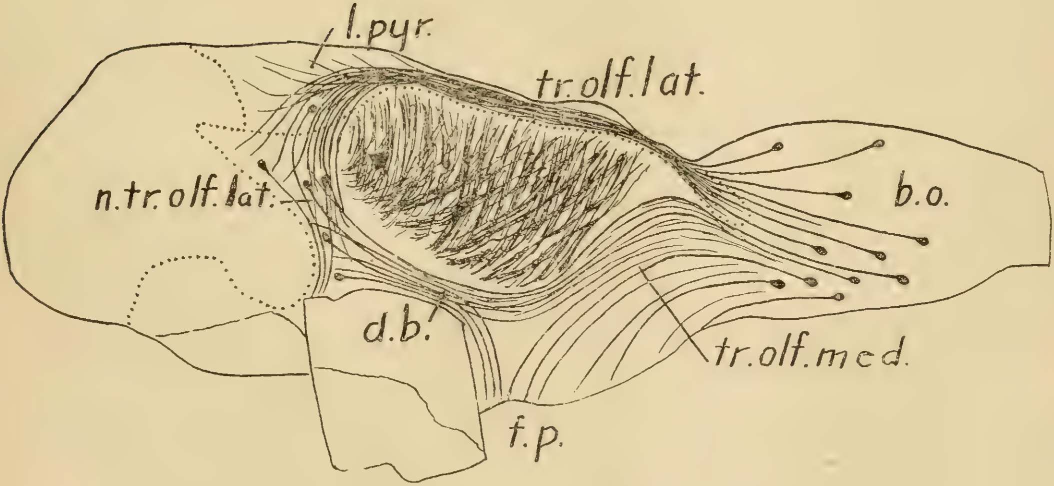
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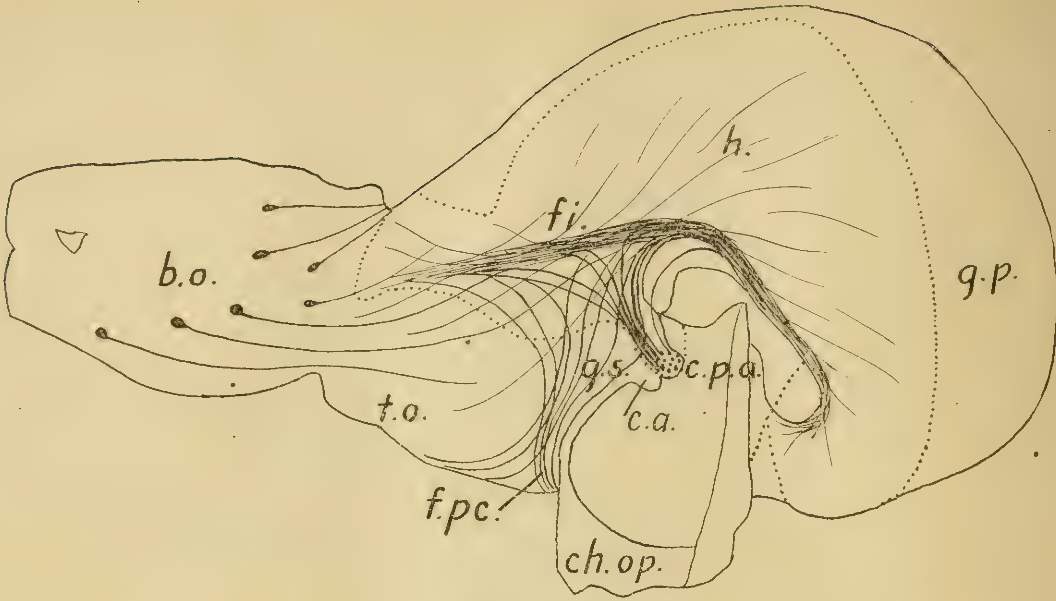

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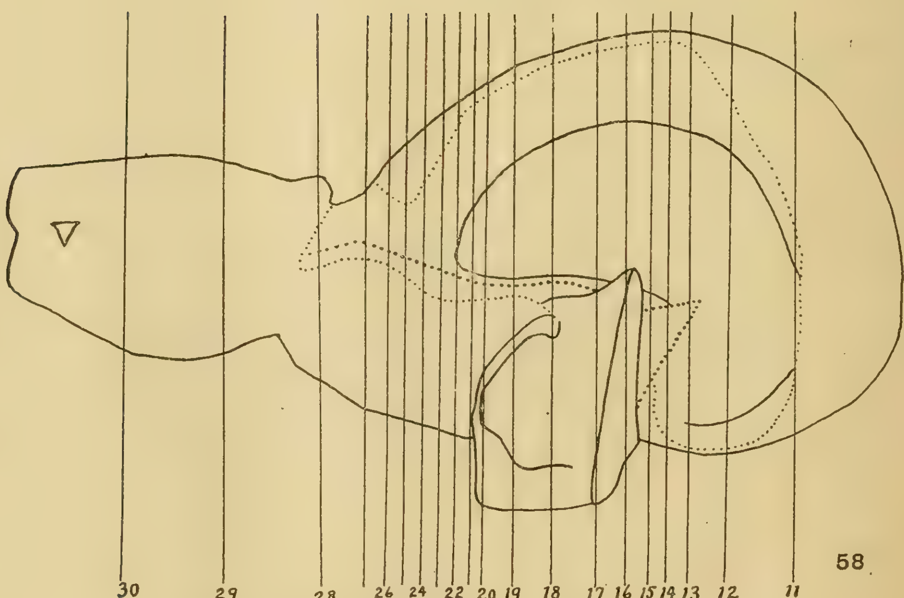

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Fig. 57 A diagram of tracts in the medial wall. Outline from figure 6. This shows especially how the fimbria system is made up of several components: olfactory tract fibers, precommissural fibers from the diagonal band, hippocampal commissure, and fornix (not drawn).

Fig. 58 Sketch of the right hemisphere after figure 10 with lines to show the position of the sections drawn in figures 11 to 30.

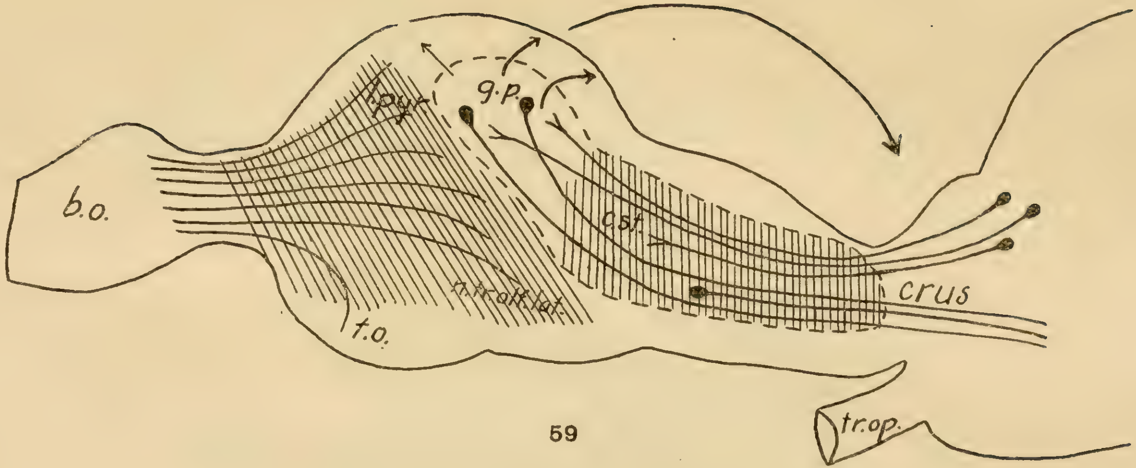

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Fig. 59 Schema of the selachian forebrain viewed from the left side. The outline corresponds to that of the forebrain in Scymnus or Heptanchus. The lateral olfactory area is shaded with oblique lines, the corpus striatum with vertical lines. The expansion of the somatic centers in the roof as general pallium is indicated by arrows and the direction of the chief expansion of the hemisphere is indicated by a large arrow. The equivalent of the pyriform lobe and the nucleus of the lateral olfactory tract lie rostral to the corpus striatum. The expansion of the pallium has been accompanied by a great elongation of this olfactory area.

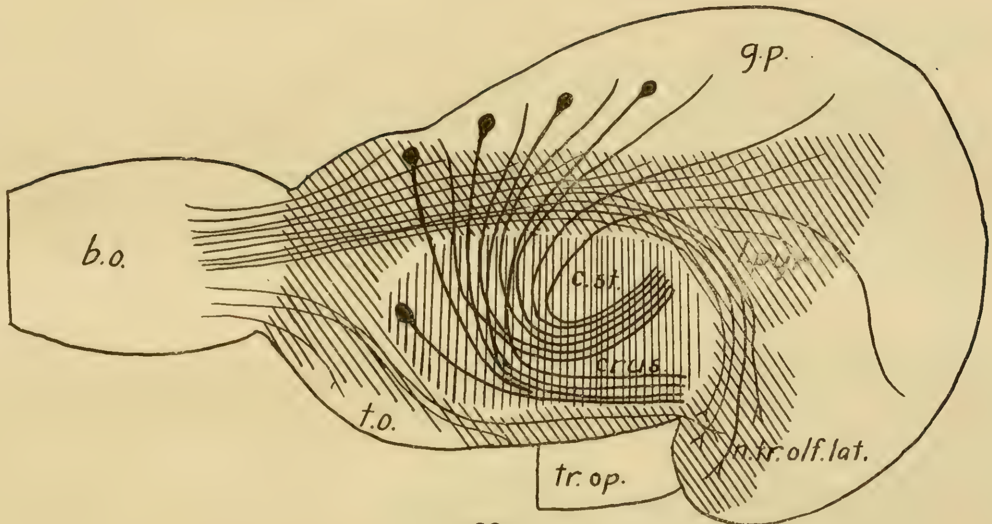

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Fig. 60 Schema of the forebrain of the turtle viewed from the left side, for comparison with figure 59. The olfactory area has been stretched over and beyond the corpus striatum but does not now form a covering of the striatum. The present condition in the turtle is such as would have been produced if the striatum had been covered by an olfactory layer and then the cells of that layer had withdrawn to the borders of the striatum so as to form a ring of olfactory centers around it.

STUDIES ON REGENERATION IN THE SPINAL CORD

I. AN ANALYSIS OF THE PROCESSES LEADING TO ITS REUNION AFTER IT HAS BEEN COMPLETELY SEVERED IN FROG EMBRYOS AT THE STAGE OF CLOSED NEURAL FOLDS

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EIGHT FIGURES

In 1913[1] a systematic study was begun on the restoration of anatomical and physiological continuity of the spinal cord severed at different ages. To the present time experiments have been carried out on three series of frog embryos and tadpoles and further work is being done on later stages. The object of this study is to obtain evidence which will aid in clearing up the conflicting results of previous investigations and especially to determine the following points: 1, whether the completely severed spinal cord will regenerate; 2, the nature of the process, if healing occurs; 3, the causes which prevent it, if it fails; 4, the origin of the regenerated elements and whether the epidermis or connective tissue play any rôle; 5, the effect of isolation of a segment of the cord upon the development of reflexes in it in the early embryo, and 6, the physiological phenomena associated with the regeneration.

Born ('97) demonstrated that complete reunion of the severed spinal cord could easily be obtained in the frog embryo at the earliest neural tube stage provided the surfaces of the wound

[1] The experiments described in this paper were carried out in the Anatomical Laboratory of the School of Medicine of Yale University. I take great pleasure in thanking Prof. H. B. Ferris for extending to me the courtesies of his laboratory for this purpose. I am indebted to the Loomis Research Fund of the Yale University School of Medicine for some of the apparatus used.

were brought into contact with one another and kept apposed until the skin cut had healed. By this means he found it possible to perform homo- and heteroplastic fusions of pieces of embryos. Harrison ('98, '02) not only succeeded in fusing halves of embryos of different species, but carried such a composite embryo through its metamorphosis. Where careful apposition of the wound surfaces is practiced, no active regenerative processes ensue. Under such circumstances the various organs heal *per primam*, the tissues fuse together and the embryos possess the normal continuity of all their structures within a very short time after the operation. On the other hand, if the spinal cord be severed and its cut edges are not brought into contact with one another, a very definite series of events ensues which tends toward the reunion of the cord. The present paper deals with these regenerative processes and the gross points of the behavior of embryos operated in this manner.

EXPERIMENTS

Method. Embryos of Rana sylvatica, 3.5 to 3.75 mm. in length, were operated upon in 0.4 per cent saline under a Zeiss binocular microscope. Anaesthesia was unnecessary as the peripheral nervous system has not as yet begun its development. With a finely pointed pair of Noyes' iridectomy scissors a cut was made in the dorsal portion of the body just behind the small projections which mark the position of the pronephroi. Care was taken to cut completely the skin of the dorsal half of the embryo, the neural tube, the notochord and the myotomes on each side of the cord in such a manner that the two portions of the body were connected to one another only by the yolk and the skin of the ventral and ventro-lateral region.

The physiological tests for interruption of the continuity of the spinal cord, so valuable in older stages, are not applicable here, as the embryos do not move. At the time of operation it is possible, however, to see the cord and notochord by slightly separating the edges of the cut and to observe the completeness of the operation so far as these structures are concerned. The

extent of the skin cut determines quite accurately the amount of separation of the myotomes. The division of the notochord is the most important criterion of the success of the cut. The sections of all embryos which have been operated upon in this manner show the exact point of severance of the notochord. This is marked by a mass of characteristic cells which have proliferated from the cut notochordal sheath. During the earlier stages of their growth, the operated embryos present a nick in the dorsal fin which macroscopically determines the location of the cut.

After operation the embryos were left in the saline for several hours. The wound surfaces became covered with epithelium in from one to five hours. In all cases the epidermis dipped down into the cleft. Until the cut has been covered by the migration of the epithelial cells, care must be taken not to shake the dish in which the embryos lie, as it is easy to break them in two during this period. The wound edges were not apposed to one another, with the result that all degrees of gaping of the cut were obtained. Individuals in which the cleft in the back was more than 0.5 mm. wide were rejected.

Embryos were killed 1, 2, 4, 7 and 18 days after the operation. Sublimate acetic was used as a fixer. Held's molybdic acid hematoxylin and congo red, Ehrlich's hematoxylin and congo red, Mallory's connective tissue method and erythrosin and toluidin blue were used in staining the sections. It was found that Held's hematoxylin gave the best results in the earlier stages and the erythrosin and toluidin blue in the older embryos.

Embryos 24 hours after operation. At this time the embryos measured from 3.75 to 4.25 mm. in length and presented a rather well developed tail-bud. A deep cleft in the back marked the location of the cut. It divided the structures of the dorsum of the body nearly to the yolk. Many of the embryos had begun to exhibit the voluntary movements which normally appear at this time. They consisted in a side to side bending of the neck. The portion of the body just in front of the cut was not involved, nor did that part of it behind the site of the wound move voluntarily. Light skin stimulation of the body anterior to the cut was quickly followed by a movement of the head. Tactile

stimulation of the posterior part of the body had no effect, but direct mechanical stimulation of the muscles of this region produced the usual response.

Sagittal sections of embryos killed at this stage demonstrate (fig. 1) that both spinal cord and notochord have been completely severed. The epidermis has grown over the wound surfaces in such a manner that a partition has been formed across the dorsal portion of each embryo, perpendicular to the long axis of the body and further separating the severed structures from one another: In all but two of the embryos both cord and notochord were separated by this ingrowth. In the two exceptions the ends of

Fig. 1 Sagittal section of an embryo killed 24 hours after operation. The central nervous system is shown in black. The spinal cord and notochord have been divided and are separated by a V-shaped ingrowth of epithelium. (Embryo VIII 81, 2-14).

the notochord had been sufficiently apposed to reheal, but the location of the cut is marked by a deeply staining, dense mass of notochordal tissue upon which the epidermal partition rests.

The epidermis covering the wound is slightly thicker than elsewhere on the dorsal surface and lies in almost direct contact with the ends of the spinal cord and notochord. It is extremely difficult to differentiate between the cells of the cord and those of the epidermis. Nevertheless, it seems probable that the latter plays no part in the regeneration of the former. This tentative opinion is based on the study of a larger series of experiments than that described in this paper. The investigation of this point is not completed but will be published in full at an early date. Elsewhere the epidermis is connected to the underlying organs by mesenchyme.

The severed ends of the spinal cord have become slightly rounded off and the canalis centralis, opened by the cut, has been closed over on both sides of the wound. This has apparently been effected by a rearrangement of the existing cells. No karyokinetic figures have been observed in this region. As yet, no nerves have grown out from the ends of the cord nor can their beginning development inside it be noted in this region. The motor roots of the spinal nerves have, however, made their appearance.

The ends of the notochord also have become rounded off, except in the two cases noted above. The proliferation of connective tissue from the notochordal sheath has begun and with the mesenchyme forms a fibrous mass attached to the epidermal ingrowth. The yolk has in each case formed a slight mound just below the site of the wound, caused by the diminution in its surface tension at this point at the time of operation.

This stage represents the period of primary repair and preparation for the active regeneration which begins shortly after.

Embryos 2 days after operation. The embryos at this time measured from 4.5 to 6 mm. in length and possessed branched gills. The cleft in the back of the animals was largely limited to the dorsal fin. All the embryos moved voluntarily by repeatedly turning the head from side to side No spontaneous movement was observed in the hinder end of the body. A few embryos exhibited a very imperfect type of locomotion. This was produced by an increase in the number and force of the side to side motions of the head which caused a swaying of the tail. Though at first purely passive, the tail muscles were excited to contraction with the continuance of the head movements. The locomotion which resulted from their action carried the embryo over short distances. The lack of synchrony between the two nervously isolated portions of the body prevented an efficient swimming motion. As soon as the head end became quiet, the tail movements diminished in force and ceased.

Gentle tactile stimulation of the anterior end of the body resulted in responses only from that end. Long continued stimulation of the region in front of the cut produced swimming

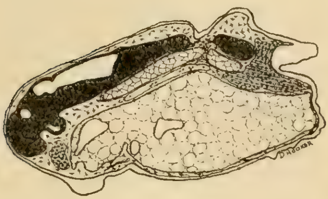
movements of the type mentioned above. Tactile stimulation of the body behind the cut caused a single reflex response. Direct mechanical stimulation of the muscles of the posterior half of the body resulted in swimming movements. The locomotion thus produced carried the embryos for considerable distances and was sustained for a longer period than that originating from the movements of the anterior end.

Sections of embryos killed at this stage show that a marked advance in development over those killed 24 hours before has occurred. The spinal cord and notochord have been here, as in the earlier stage, completely severed (fig. 2), but the partition of epidermis no longer separates the ends from each other. The tension on the skin accompanying the increase in length of the tail, noted by Harrison ('98), has pulled the ingrowth of epidermis nearly flush with that of the rest of the body, so that the cleft in the dorsal surface of the body is largely limited to the fin. The consequent movement in the dorsad direction of the bottom of the epidermal partition has drawn with it a mass of connective tissue, derived from the notochordal sheath and attached to the under surface of the skin (fig. 3), to a position between the severed ends of the spinal cord. This serves as a mechanical obstruction to the restoration of the anatomical continuity of the cord almost as effective as that previously formed by the epidermal ingrowth. This tissue is in sharp contrast to the mesenchyme found elsewhere in the body by reason of its closely interwoven fibers and the large number of cells which it contains. It is directly continuous with the notochordal sheath on both sides of the cut.

In the spinal cord itself the ventral motor tracts have begun to appear. The fibers arise from cells situated in the ventral portion of the cord, especially in the anterior half of it. Many of the cells lying near the canalis centralis exhibit different phases of mitosis. The karyokinetic figures are not localized in any particular region of the cord and are no more numerous than in normal embryos of the same age.

Processes extend from each end of the cord toward the other, arising from the motor tracts. That they are nerve fibers is

proved by the fact that they contain neurofibrillae which are readily seen in sections stained with Held's hematoxylin or toluidin blue. The fibers arising from the anterior portion of the cord pass caudad and dorsad, those from the posterior piece cephalad and dorsad. This deflection from the straight course is necessitated by the interposed mass of notochordal sheath tissue, which it is seemingly impossible for the nerves to penetrate at this stage. The number of fibers from each end of the



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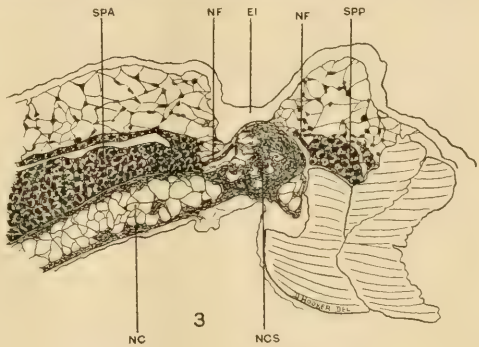

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Fig. 2 Sagittal section of an embryo killed 2 days after operation. The epidermal ingrowth is partially withdrawn. Both spinal cord and notochord are divided and short nerve fibers are developing from each piece of the cord. The tail is not shown in the figure. (Embryo VIII 67, 3–12).

Fig. 3 From the same embryo as the preceding figure. The notochord (*N.C.*), the mass of notochordal sheath tissue (*N.C.S.*), the epidermal ingrowth (*E.I.*), the anterior (*S.P.A.*) and posterior (*S.P.P.*) pieces of the spinal cord, and the motor nerve fibers (*N.F.*) growing from each end of the latter are shown. (Embryo VIII 67, 3–18).

spinal cord is small, varying from five to fourteen in the different embryos. Their course is in all cases irregular. At first they pass either caudad or cephalad, according to the end from which they rise, then turn and apparently follow along the outside of the notochordal sheath tissue. Though their course is tortuous, they are directed toward the opposite end of the spinal cord. The longest fiber observed measures 63.75 μ in length. In no case are any of the normal peripheral nerves deflected from their course toward either end of the cord.

From the evidence afforded by the sections, it would seem that the increase in length of the spinal cord has not kept pace

with the growth of the embryo as a whole. In consequence, its cut ends have been drawn away from each other in the preceding 24 hours development. As the initial separation of the two pieces of the cord is different in each embryo, dependent on the gaping of the wound after operation, a comparison of the distance between their cut surfaces in the different stages gives no valid results. The position of the developing spinal ganglia in relation to the ends of the cord does, however, offer a criterion by which this may be demonstrated. In this stage the ganglionic anlagen in the anterior two-thirds of the body have become separated from the cord and lie in more intimate connection with the myotomes than with it. The distance between the most caudad ganglion anlage in front of the cut and the end of the anterior portion of the cord added to that between the cut surface of the posterior portion and the first ganglion anlage caudad to it is less than between any two ganglia of one side. As no degeneration of the cord has taken place at its cut surfaces, its retraction past the ganglionic anlagen as fixed points seems to be the only valid explanation of the shortening that has occurred.

The 48 hour stage marks the first step in the establishment of the primary reunion between the two pieces of the spinal cord. It is characterized by a procedure of the same nature as that seen in the development of the peripheral nerves, namely, the outgrowth of motor nerve fibers. In this case, however, they grow out from the ends (descending and ascending processes) rather than from the sides (collateral processes of Coghill) of the cord.

Larvae 4 days after operation. Four days after operation the larvae measured from 6 to 7.2 mm. in length. The body had begun to assume the rounded, tadpole form due to the rapidly progressing absorption of the yolk. The external gills were well developed and the tail fins had become transparent. The only external mark of the operation was a nick in the dorsal fin which extended down to, but not into, the body. All the tadpoles were active and swam voluntarily. Tactile stimulation of either end of the body caused the larvae to swim. In the majority of cases the swimming movements, though not entirely normal, were

well coördinated. Some, however, had difficulty in locomotion. All of these latter were deformed, the posterior end of the body being bent ventrally on the anterior at the point of operation. The varying amounts of gaping of the wound appear to have little effect on the appearance or behavior of the animals as long as a considerable quantity of yolk is present. This provides a support for the body and preserves its normal form. The support thus given is removed with the absorption of the yolk and bodily deformities, which were not previously noticeable, then come to light. Many of the slightly abnormal larvae subsequently overcome this, but where the amount of bending exceeds a by no means definitely determinable maximum, the deformity increases with further growth. These embryos and tadpoles will be discussed in detail later. At the stage under consideration (4 days after operation) the amount of deformity exhibited by even the most abnormal larvae was slight.

Sections of larvae killed at this stage show that the withdrawal of the skin from its earlier position between the surfaces of the cut has progressed so far that it no longer forms even a partial barrier to the regeneration of the cord (figs. 4 and 5). The mass of notochordal sheath tissue is still interposed between the cut ends of the spinal cord, but its fibers have become somewhat less closely packed about the periphery.

Evidence is at hand that a further retraction of the ends of the cord from the site of the cut has occurred. With the exception of the first and second pairs, the long axis of the spinal ganglia in this stage is normally directed ventrally and caudally. In these operated embryos, the first two pair of ganglia caudad to the cut (the 4th and 5th or 5th and 6th, as the case may be) have their long axes directed ventrad and cephalad. The sensory axones of the ganglion cells make their connections with the cord shortly after the 48 hour stage. The upper ends of the ganglia are thus attached to the cord and the lower ends to the myotomes. With the increase in length of the embryo, accompanied by the gradual retrogression of the cord ends from the cut, these ganglia have been pulled over to their new position. No such criterion of the shortening of the anterior end of the cord is

furnished by the position of the ganglia there, as the tension of the retrogressing cord would not so materially change the direction of their long axes.

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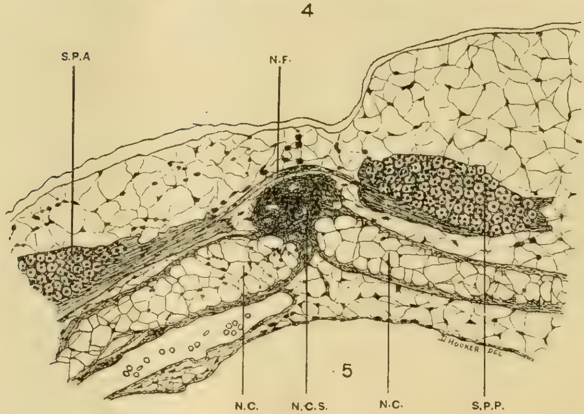


Fig. 4 Sagittal section of an embryo killed 4 days after operation. The epidermal ingrowth has been entirely withdrawn. The motor connections between the two ends of the cord have been established and the sensory nerves are beginning their development from the posterior piece. (Embryo VIII 68, 3–18).

Fig. 5 From the same embryo as the preceding figure. The lettering is the same as in figure 3. The motor connection between the two ends of the cord is shown. (Embryo VIII 68, 3–15 to 20).

Numerous, long nerve fibers, in all cases containing neurofibrillae, are given off from both segments of the cord. They pass out of the cut ends from the ventral motor tracts. The fibers from each segment of the cord branch freely and interanastomose with each other and among themselves. Some of the nerves from the anterior piece of the spinal cord send branches to innervate the first three myotomes behind the cut. The main fibers in each case are directed toward the posterior piece. The ventral motor fibers from the posterior segment of the cord grow

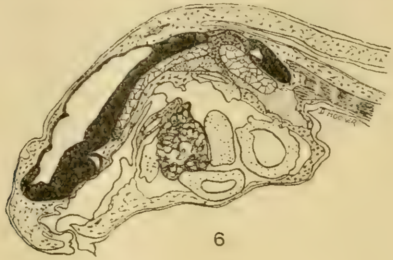
cephalad and pass the fibers from the anterior end. They do not branch to any extent and do not innervate the myotomes. In addition to these fibers from the ventral region of the cord, the posterior segment sends out a few small fibers, containing neurofibrillae, toward the rostral end of the embryo. They are apparently derived from the dorso-lateral or primary sensory tract. The anterior segment of the cord has no nerve fibers which arise from this region.

The nerves of the motor tract are less scattered than in the 24 hour stage. They are grouped into two heavy strands which connect the ends of the cord and which pass along the upper portion of the mass of notochordal sheath cells, penetrating it in some places. Interwoven with the distinctly nervous fibers are others which are narrow and granular in appearance. They are connective tissue fibers from the mesenchyme cells through which the nerves have grown.

These tadpoles illustrate the second phase of the primary reunion of the cord segments. The motor apparatus has bridged the gap and the nerves which will later establish the sensory connections are just beginning their development. It is impossible to determine whether the nerves from the anterior segment have established their connection with neurones in the hinder end of the cord or whether those from the posterior segment have reached their goal in the anterior end. The slightly imperfect coördination of the two ends does not make it seem probable that they have done so.

Larvae 7 days after operation. The larvae at this time measured from 7.75 to 9 mm. in length and were typically tadpole-like in shape. The yolk had been entirely absorbed and, in consequence, the deformity of many of the abnormally shaped larvae had increased. Those tadpoles which were not deformed presented only a slight nick in the dorsal fin to show the location of the cut. Physiologically, the undeformed tadpoles were normal in every respect. They swam, reacted to stimuli and ate as well as did the controls. The deformed larvae had difficulty in locomotion due, in part, to the abnormal position of the tail and also to the lack of coördination between the two portions of the body. None of these were killed at this time.

Sections show that both spinal cord and notochord had been completely severed (figs. 6 and 7). The mass of tissue which has proliferated from the notochordal sheath is less extensive than in previous stages and appears to be undergoing resorption.



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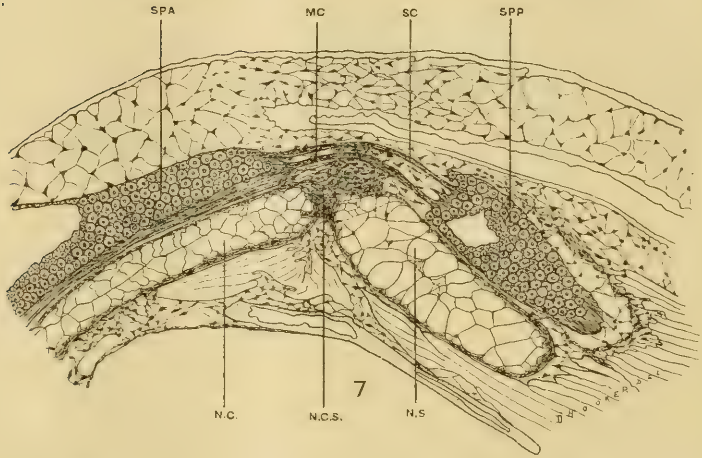

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Fig. 6 Sagittal section of an embryo killed 7 days after operation. The primary reunion of the cord ends is completed by motor and sensory connections. (Embryo VIII 63, 14–11).

Fig. 7 From the same embryo as the preceding figure. The lettering is the same as in figures 3 and 5. The motor (*M.C.*) and the sensory (*S.C.*) connections are shown. (Embryo VIII 63, 14–11).

Through the looser tissue of the upper portion of this mass pass some of the fibrous connections between the ventral portions of the two cut ends of the spinal cord. These connectives are bundles composed largely of nerves and connective tissue fibers. The nerves are continuous with the ventral fiber tracts of both

portions of the cord and their origin from neuroblasts situated behind the cut ends may be observed in some cases. None of the nerves arise from nerve cells at the cut surfaces. The connective tissue fibers, identifiable by their granular appearance, are found in large numbers in the middle of the gap. Toward the anterior end of the cord they have left the position among the nerve fibers occupied by them slightly further back and lie entirely outside the bundle. Their place is taken by a number of very fine, branched processes which arise from the epithelial cells of the canalis centralis of the anterior stump. For some little distance in front of the actual end of the cord, these cells are found in large numbers lying on all sides of the central canal. Frequent mitotic figures are to be seen among them. The cells situated anterior to this mass and those near the tip of the stump show processes of the type noted above. Those from the cells nearest the end of the cord extend, in this stage, a short distance into the fibrous bundles.

Though the mitoses found among the epithelial cells of the canalis centralis are not sufficient to account for their extraordinary number, it is apparent that they are rapidly proliferating. Examination of the position of the spinal ganglia and the sensory roots in relation to the cord reveals that, following the retraction of the cord, a progression of its anterior end has occurred. In one of these embryos, VIII 65, the center of the last spinal ganglion of the anterior segment lies 131.25 μ behind the point of entrance of its sensory root into the cord. As in normal embryos at this stage the same relative measurement rarely exceeds 90 to 95 μ, it is evident that the cord has been pulled forward to some extent since the sensory root became attached to it. On the other hand, the end of the anterior piece of the cord is 304 μ behind the point of entrance of this sensory root. As the greatest distance between the end of the cord and the entrance of the sensory root of the next cephalic ganglion found in any of the embryos in this or preceding stages measures only 131 μ, it is further evident that the spinal cord has increased somewhat in length since the 4 day period. The mass of epithelial cells of the central canal thus seems to designate the

position of a growing area by means of which the length of the cord is increased. No such mass of cells is found in this stage in the posterior segment.

The tip of the anterior stump of the cord presents another significant step in the regenerative processes. From the time of the initial rounding off of the cut surfaces during the first 24 hours after operation, no change beyond the protrusion of developing neuraxes and a few supporting fibers has taken place on either end. In this stage, however, some of the cells at the end of the anterior stump are seen to have migrated along the numerous fibrous connections bridging the gap. These cells, which may be differentiated from those of the mesenchyme by their large, round, darkly staining nuclei, are certainly neuroblasts. They appear to have no processes and are supported by and intermingled with the nerve and ependymal fibers. They are found only in that portion of the fibrous connection which contains the processes of the neural supporting cells. None have as yet migrated from the posterior stump.

Somewhat dorsal to the bundles of fibers which have been discussed, lies a second series of nervous connections between the two ends of the cord. These consist of smaller bundles of neuraxes and connective tissue fibers, of which the former arise from the lateral portions of the dorsal half of the cord. They are easily identifiable as nerve fibers by the neurofibrillae which they contain. They may be regarded as establishing connections between the giant cell areas of the spinal cord and are, therefore, probably sensory in nature. Posteriorly their origin is distinct from that of the motor fibers. Anteriorly they enter the mass of short ependymal fibers arising from the whole cut surface of the cord.

The 4 day stage is marked, then, by the completion of the primary reunion of the stumps and by the beginning of those processes which will ultimately restore the form of the regenerated cord.

Larvae $2\frac{1}{2}$ weeks after operation. In the week and a half which elapsed between the last stage described and the present one, the tadpoles increased in size until they measured 14 to 16 mm.

in length. During their growth the body had rounded out and the portion of the dorsal fin anterior to the cut had disappeared. The site of the cut was marked only by a slight crease in the dorsal surface of the body. The behavior of these individuals was in every way normal.

Sections of larvae killed at this time demonstrate that the spinal cord and notochord had been severed in all cases. The apparently normal individuals exhibit the final steps in the complete restoration of the anatomical continuity of the cord.

In the tadpoles showing the stage following the one last described, the two cut ends of the cord are united by a dense mass of fibers. They are of three types: 1, neuraxes, rather broad and longitudinally striated by reason of the neurofibrillae which they contain; 2, connective tissue fibers, granular in appearance; and 3, a large number of the fine, branched fibers arising from the epithelial cells of the canalis centralis. The majority of these last appear to come from the anterior stump of the cord, though many arise from the posterior. They are by far the most numerous of the three types of fibers and bind the motor and sensory connections into one heavy cable. Their growth into the fiber mass connecting the two ends of the cord is accompanied by the partial exclusion of the connective tissue fibers from it. This exclusion is complete where the neuroblasts have migrated into the network of neuraxes and ependymal fibers. Where this has occurred, the connective tissue forms an enveloping membrane over the outside of the neural elements, easily distinguishable from them by the granular nature of the cytoplasm and the smaller size of the nuclei.

Though the great bulk of the regenerated area is composed of the two types of neural cell processes, an increase in the number of neuroblasts which have migrated out from the cord is to be noted. In this stage, the posterior stump has begun to contribute these cells. Further evidence is presented by these tadpoles that the two stumps of the cord are approaching one another by a process of subapical growth, accompanied by the progressive canalization of the group of epithelial cells about the ends of the canalis centralis. Positive proof that the central

canal is being lengthened by the continuation of its lumen into this mass of cells is lacking, but the conformation of its supposed growing point and the nature of the canal at the point of union in the completely reunited spinal cord is in favor of this supposition.

Tadpole VIII 73 (fig. 8) is typical of those in which the restoration of the anatomical continuity of the cord is complete and will be described in detail as such. Four things only give internal evidence that the cord has been cut: 1, its slightly smaller diameter at the regenerated area, 2, the irregular course of the canalis centralis, 3, the uneven distribution of cells and fiber-tracts

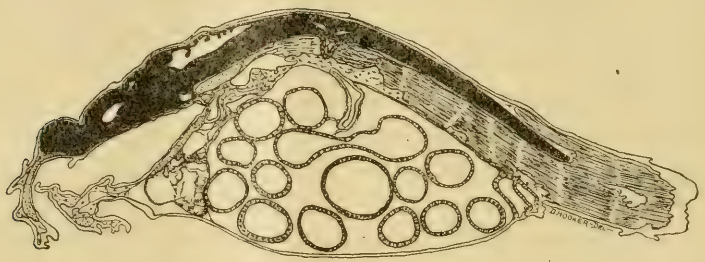

Fig. 8 Sagittal section of an embryo killed 18 days after operation in which the spinal cord has completely regenerated. Note the ventral direction of the two portions of the canalis centralis shown. The original cut passed between them. (Embryo VIII 73, II 2–3).

and 4, a deviation in the notochord which marks the site where it was severed. The skin and connective tissue lying above the cord have healed so completely that no indication of the original wound is given, unless it be a slight fold of the former.

The regenerated area of the spinal cord has a diameter which at its most constricted point is 32μ less than that of the cord on either side. From this narrowest region the diameter gradually increases on both sides to that of the normal cord. It is impossible to accurately measure the length of the regenerated cord, as only in the center does it present any variations from the normal structure. This region, however, is about 300μ long.

The canalis centralis of each end of the spinal cord bends ventrad to the point of juncture. For some distance on either

side of this point it presents certain irregularities in its course. The unregenerated canalis centralis is regular in outline, somewhat oval in cross section and lies in the center of the cord. The regenerated canal is rather tortuous in its course, varies from nearly a circle to a very narrow, parallel-sided slit in cross section and does not occupy a constant position in the cord. It is, however, single. In no case has any tendency toward multiplication of the central canal been observed in these operated embryos and tadpoles.

The third indication that the cord has been severed is to be found in the distribution of cells and fibers in the regenerated area. In the uninjured portions of the cord, the cells form a definitely placed group about the canalis centralis, sharply delimited from the fiber tracts on the periphery of the cord. In the regenerated portion, the regular outline of the cell area is broken and the thickness of the area itself varies greatly in sections of the cord which are quite close together. In some places, the cells lie at the periphery of the cord. Where this is the case, they are arranged in no definite manner and are found among the fibers which normally lie on the outside of the cord. In other places, the bulk of the cells lies to one side of the canalis centralis, the opposite side being occupied chiefly by fibers. This is notably the case where the central canal bends laterally or ventrally from its normal position. Furthermore, the nearer one approaches the supposed point of junction of the two ends of the cord, the fewer become the neuroblasts which are found there. It would appear that the normal number of cells is not present and that their arrangement is disturbed by the lack of definite separation of the cell and fiber areas. Whether or not the number of neurones in this region would in time increase to normal is at present a matter of conjecture.

The notochord also gives evidence of having been cut. The mass of notochordal sheath tissue, which formed a prominent feature of the environment of the cord stumps in earlier stages, has here completely disappeared. The two ends of the notochord have fused, but the point of fusion is marked in tadpoles of this age by greater or less deviations from the straight course normally

taken by it. In tadpole VIII 73, this deviation takes the form of a sharp, lateral V-shaped turn toward the left. Owing to the fact that the plane of section of this tadpole is not exactly perpendicular, only the tip of this bend has been cut in the section figured.

DISCUSSION

It is evident from the experiments that, under favorable conditions, the spinal cord of frog embryos will regenerate after having been completely severed in the cervical region during the stage following the closure of the neural folds. The primary reunion is effected by the development of nerve fibers which bridge the gap and establish the physiological continuity of the cord. Such rehealing was reported as far back as 1849 by Brown-Séquard. Two months after he had completely severed the spinal cord in the thoracic region of 2 adult pigeons, he found white fibers (*'filets blancs'*) traversing the tissue which united the cut ends of the cord. These were identified by M. Follin (Brown-Séquard, '50) as nerve fibers, after the microscopic examination of the regenerated area in a similarly operated pigeon killed 3 months after operation. Harrison ('10) has observed the beginning of the same process as that described in this paper. After removal of relatively large portions of the spinal cord from frog embryos in the closed neural fold stage, nerve fibers grew from each of the cut surfaces toward the other. Though these nerves did not reach their supposed objective points before the embryos were killed (4 days after operation), it is evident that their outgrowth represents an attempt at restoration of the continuity of the cord.

The rôle played by both ends of the severed cord in the regenerative processes is significant. It was found that the anterior piece of the cord initiated the various steps in the restoration somewhat in advance of the posterior. This is in full accord with the work of Coghill ('13 and '14), who has shown that differentiation in the spinal cord begins in its rostral end and proceeds caudally. Nevertheless, the posterior end does contribute elements to the regenerated area. Opposed to this

observation are the results of Masius and van Lair ('69), who claim that the caudal stump takes little or no part in the regeneration of the cord in adult frogs. Brown-Séquard presents no evidence as to the origin of the nerve fibers in the regenerated area in his pigeons, but states ('51), as do Masius and van Lair, that the spinal cord resembles a nerve in its method of regeneration. While it is undoubtedly true that the individual nerves which make up the cord regenerate in the usual manner, the essential differences between the cord and a nerve make an exact comparison of the regeneration in the two a dangerous one. Though the descending processes of the motor neurones in the anterior stump of the cord grow caudad and the ascending processes of those in the posterior piece grow cephalad, they do not unite with one another, but pass on to establish their connections independently. There is no autoregeneration in Bethe's sense of the term.

Indeed, it is very doubtful if the term 'regenerative' may be applied to the nerve development seen in the embryos under discussion. There is no degeneration preceding the growth of the neuraxes, for no nerves had developed at the time of operation. We are, therefore, dealing here with a normal morphogenetic process. The spinal cord as a whole regenerates, the neurones do not.

This fact throws an added importance on the observations of the growth of the motor and sensory fibers, as their relative time of appearance and point of origin at the cut surfaces represent the nature of their normal development. It is thus evident that the descending process of a motor neurone in the lower cervical region of the cord begins its development and consequently establishes its centrifugal connections before its caudally situated neighbor has established its centripetal connections. It is further evident that the caudally progressing differentiation of the sensory tract is brought about by the successive additions of cephalically directed axones from the sensory cells, not by the development of dendrites toward the caudal end of the cord to establish connections with lower neurones. This confirms the results of Coghill ('14) in Amblystoma.

Coghill's discovery ('13) that the myotomes receive their primary innervation from collaterals of the descending processes of the motor cells in Amblystoma is also corroborated by the conditions found in these frog embryos.

The primary reunion of the cord by the growth of fibers between its two ends, though accompanied by the establishment of physiological continuity, does not restore its anatomical structure to a condition even approaching the normal. The experiments demonstrate that a regular series of events must take place before this can occur. These steps to complete regeneration of the cord are found to succeed one another in regular order, though the end of one process usually overlaps the beginning of the next.

The outgrowth of fibers from the epithelial cells of the canalis centralis plays an important part in the form restoration of the cord as they provide the framework of the regenerated area. They appear almost concomitant with the completion of the sensory nerve fiber connection between the two stumps of the cord and arise from cells situated near the closed ends of the canalis centralis. Closely following on this process, begins the wandering of neuroblasts into the framework of nerve and ependymal fibers. The number which migrate into the fiber mass is less than that found in the completed cord and they are not the ones which have given rise to the neuraxes present in the regenerated area at this stage. Caporaso ('89) believes that, in regeneration of the cord in tritons after amputation of the tail, the epithelial cells of the canalis centralis divide to form the nerve cells of the new cord. That such is not the sole source of the neuroblasts in these frog embryos is certain, but it is very probable that from these canalis centralis cells some do develop.

The principal factor in the structural restoration of the regenerated cord appears to be the elongation of the canalis centralis and its epithelial cells in each stump. Just behind their apices, the two ends of the canalis centralis present a slight widening of the lumen surrounded by a dense mass of its epithelial lining cells. Their number is much greater here than elsewhere in the cord and it is evident that rapid proliferation is going on. In

spite of this, the number of mitoses to be found is too small to account for the mass of cells produced. An explanation for this is not at hand. A similar discrepancy between the number of mitoses found and the number of cells produced has been noted by Caporaso ('89) in the regenerating cord of triton. The position of the mass of proliferating cells indicates that any increase in the length of the canalis centralis and the consequent elongation of the cord stumps does not take place at the tip, but just behind it, by the interpolation of elements.

After the cord has been restored both in structure and form, it contains all the essentials elements normally found in it, though the number of nerve cells is somewhat smaller. The regeneration has been effected by the growth of a new piece of cord connecting the cut ends of the original one. The consequent increase in length is compensated to some extent by the separation of the cord ends during the growth of the earlier stages. Nevertheless, the distance between the first pair of spinal ganglia in front of the cut and the first pair behind is increased by the original gaping of the wound. That the interposed area has developed entirely from the structures of the original cord is well assured. The only possible extraneous sources for the elements of the new section of the cord are the epidermis and the surrounding connective tissue. The first, probably, and the second, certainly, does not enter into the regenerative process.

The absence of multiple central canals in the operated embryos is of interest in the light of previous investigation. Born ('97) noted their presence in some of his composite frog embryos. Fraisse ('85) and a number of others have found the same condition in the regenerated tails of lizards. In a recent paper ('14), Waelsch has attempted an analysis of multiple central canal formation in the chick, following the introduction of Scharlach R. in oil under the medullary plate. He concludes that the well known power of Scharlach R. to stimulate epithelial growth holds good in the case of the epithelial cells of the central canal, stimulating them to overgrowth which results in the multiplication of the canal. Weber ('15), in commenting on Waelsch's paper, attributes this phenomenon to any stimulus,

even distilled water, which alters the environment of the spinal cord. Fischel ('14) notes the occurrence of multiple canals in well developed salamander larvae after stab wounds in the cord. In spite of the general unanimity of opinion that very slight stimuli will produce multiple canales centrales, no cases have been found in the course of these experiments. The possibilities for abnormal development were, in the nature of the case, great. In some embryos the two cut ends of the spinal cord were markedly displaced laterally. Nevertheless, the process of restoration of the cord proceeded in the same manner as in those with more perfect alignment and the central canal did not reduplicate. The cause for multiple canalis centralis formation thus seems to be dependent on other conditions than mere injury to the cord.

The relationship between the behavior of these frog embryos and the state of the anatomical connections between the ends of the severed spinal cord is of interest, especially in reference to the recent work of Coghill ('09, '13 and '14) and of Herrick and Coghill ('15). These investigators have carefully analyzed the reflex mechanism of Amblystoma and have demonstrated the developmental correlation between the nervous connections and the behavior of embryos of this animal. They have found that the sensory-motor connection is first established by the ventral commissures of the upper portion of the spinal cord and the lower portion of the medulla. Thus a stimulus applied to one side of the embryo will find its first motor expression in the myotomes of the opposite side. This crossed reflex arc requires, for the first swimming movements of Amblystoma, a complete and continuous chain of motor and sensory neurones connected with one another only at the anterior end of the embryo.

The experiments show that only on fulfilment of these requirements does the operated frog embryo become completely coördinated. This is in the stage 7 days after operation. But this is not the first stage in which these frog embryos swim. Four days after operation, the motor tracts are connected but the sensory are not, nevertheless the embryos swim in a very nearly normal manner. It is conceivable, in terms of the reflex mechan-

ism of Amblystoma, that an exteroceptive stimulus in front of the cut should excite a motor reflex in the myotomes of the opposite side, which would follow down the motor connection into the otherwise nervously isolated tail. A proprioceptive stimulus set up by the contraction of the myotomes in the anterior end of the body could then start a motor response in the side originally stimulated and thus cause a swimming movement. But an exteroceptive stimulus to the posterior end of the body causes a swimming response and there are no sensory connections between it and the anterior end. Furthermore, in the 2 day stage, the embryos will swim, though very imperfectly, if the head movements become sufficiently vigorous. As yet no anatomical basis for these phenomena is at hand. It is possible that the independent motion of the hinder end of the 4 day embryos is effected through axone reflexes. It must be remembered in this respect that some of the myotomes behind the cut are innervated by motor nerves from the anterior end of the cord in this stage.

The following hypothesis is offered as a possible explanation of the swimming movements exhibited by the 2 day stage. In a previous paper (Hooker, '11), it was noted that an increase in tension of the skin over a myotome causes it to contract. When the head of an embryo is bent toward one side, it causes increased tension of the skin over the opposite side of the posterior half. If this stimulated the myotomes of that side to contraction, a condition similar to Coghill's S-reaction would result. The return movement of the head would cause the same procedure on the other side of the embryo. It is possible that repeated movements of the head should, by summation, excite the myotomes to contract alternately on the two sides of the body. This would give rise to a very primitive type of swimming movement. However this may be, no definite conclusions can be drawn legitimately until the correlation of anatomical structure to behavior has been as thoroughly investigated in the frog as it has in Amblystoma.

THE FAILURES

Under this heading may be grouped those cases in which, for one reason or another, the spinal cord has failed to reëstablish complete anatomical continuity. There are two principal causative factors in this failure: excessive separation of the cut ends of the cord and the interposition of mechanical obstacles. These two factors are frequently found associated with one another.

As has been noted already, some embryos present abnormalities in body form following the absorption of the yolk and, in most cases, the deformity increases with further growth. It is chiefly characterized by the ventral bending of the hind part of the body on the front. As a result, the two ends of the spinal cord become widely separated from one another. The regenerative processes begin by the outgrowth of nerve fibers, as in the more favorable cases, but the establishment of primary reunion between the cord ends is rare. The developing nerve fibers have a tendency to remain in bundles, without spreading, for some distance from the end of the stump. In those embryos in which primary reunion of the cord is effected, the nerves remain grouped across the gap, but where the distance between the cord ends is unusually great, spreading of the fibers occurs. They grow in all directions and branch frequently. Some of the branches occasionally innervate muscle tissue in the vicinity, the others lose themselves in the mesenchyme. In certain cases, a few fibers may reach the other end of the cord, but it is the exception to find nervous connections between the two stumps. The other steps toward complete form restoration of the cord proceed even in the absence of primary reunion. Neuroblasts migrate into the fiber bundles to some extent and the cells of the central canal multiply in number. These processes seem to continue for a time and then to cease.

The notochord provides the most effective mechanical obstruction to the restoration of the cord. In many of the deformed tadpoles, one end of the notochord is found turned up between the ends of the spinal cord. The upturned end of the notochord is usually connected with the skin by a mass of tissue which has proliferated from its sheath and which effectually

deprives the cord of access from the front of the body to the hinder end. In such cases also, the regenerative processes in the cord begin, but cease after a time. The elevation of one end of the notochord is usually accompanied by bodily deformity of the type generally found in these embryos and, in consequence, the mechanical obstruction is combined with excessive separation of the cord stumps. Either factor may, by itself, prevent re-establishment of the continuity of the cord.

In older animals, especially adults, the connective tissue becomes a factor in preventing regeneration by strangling the cord. This has been noted by several writers. In the embryos under discussion, however, the mesenchyme plays no such rôle.

SUMMARY

1. Regenerative processes in the spinal cord severed in the cervical region in frog embryos at the stage following the closure of the neural folds will reëstablish its anatomical and physiological continuity under favorable circumstances.

2. When the cut ends of the spinal cord are brought into contact with one another, healing *per primam* results. When the wound surfaces are not apposed, reunion and return to nearly normal form and structure are brought about by the following steps: (a) the development of nerve fibers from the motor cells of each segment of the cord, (b) the growth of sensory axones from the cut surface of the posterior stump, (c), the outgrowth of fibers from the epithelial cells of the canalis centralis of either end of the cord, (d) the wandering of neuroblasts into the fibrous net between the cut ends from both stumps of the cord, and (e) the elongation of both ends of the spinal cord toward each other by the proliferation of epithelial cells of the canalis centralis and the consequent lengthening of the canal itself.

3. The elements entering into the regenerated portion of the spinal cord are derived entirely from the original cord. The surrounding connective tissue plays no rôle in the rehealing process. The epidermis probably takes no part in it.

4. Complete reunion of the cord may be prevented by the interposition of mechanical obstacles to regeneration or by the too great separation of the cut ends of the spinal cord from one another.

5. The tadpoles present a normal behavior as soon as motor and sensory connections have been established between the cord stumps.

6. Multiple canales centrales have not been observed in the reunited spinal cords of these embryos.

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ON THE RHINENCEPHALON OF DELPHINUS DELPHIS, L.

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FIFTEEN FIGURES

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INTRODUCTION

The brain of the common dolphin is characterized by the entire absence of the olfactory tracts and bulbs, and hence the dolphin is completely anosmatic. It was in 1878, that Broca first applied the terms osmatic and anosmatic to the Mammalia as a means of classifying them according to the relative state of development of their entire olfactory apparatus. In the group of anosmatic Mammalia he placed the Primates, Cetacea, and Carnivora pinnipedia; leaving all others in the osmatic group. Later Turner ('90) made the subdivisions macrosmatic, microsmatic and anosmatic. In the macrosmatic forms he included the Ungulata proper, the Carnivora fissipedia, and, indeed, the majority of mammals. In the group of microsmatics, or those having the olfactory system relatively feeble, he placed the Carnivora pinnipedia, the whalebone whales, apes and man; while under the anosmatic group were placed the dolphins, and

with some uncertainty, due to lack of definite information, the toothed whales in general.

As is well known, the Cetacea, as a result of their conformation to an aquatic mode of life, have undergone many changes in their structural peculiarities, but in no system perhaps are these changes more striking than in the organs concerned with olfaction. In the adult animals, the turbinates are relatively much reduced in size, the cribriform plate of the ethmoid is imperforate or may have only a single pair of openings, while the olfactory bulbs and tracts are represented by slight remnants or disappear entirely. The whole apparatus for the sense of smell is much reduced, thus rendering very appropriate the terms microsmatic and anosmatic to the different members of this order. Whether the anosmatics, like other mammals, have olfactory tracts and bulbs during fetal life, has not been carefully studied but it is certain that they lack them entirely in the mature animals. Thus, as stated above, there is not the slightest trace of these structures in the adult dolphin's brain.

Because of the disappearance of these external portions of the rhinencephalon, it has been interesting to study the more centrally placed parts of the olfactory mechanism, in order to see the extent of their regression. The brain of the dolphin has been studied from the same point of view by Broca ('79) and Zuckerkandl ('87). Their observations, however, were restricted for the most part to the external form and gross relations.

MATERIAL STUDIED

At the Frankfurt Neurological Institute, conducted under the direction of Professor Edinger, to whom I am greatly indebted, during the summer of 1914, I had the opportunity of examining thin sections of the brain of an adult dolphin. The sections were cut serially, and every third section stained by Weigert's myelin method. Each section was mounted on a separate plate of glass and covered with gelatine by the method worked out in the Frankfurt laboratory. In addition, five hemispheres, preserved in formalin, were available for gross study. These brains were

given to the institute by H. I. H. Prince Alexander of Oldenburg, and came from the Black Sea in the Caucasus. The sections were studied for the most part with a hand lens, or the unaided eye, and the use of the compound microscope was resorted to, only for finer details. The drawings of the sections were made with the aid of the Edinger projection drawing apparatus.

MAMMALIAN RHINENCEPHALON

The several parts of the brain which are generally considered to belong to the olfactory mechanism may first be mentioned. It is agreed that the bulbus olfactorius, the tractus olfactorius coming from it, and the region of the lobus olfactorius where this tract ends, are the most certain parts. Since the studies of Broca and of Zuckerkandl, the hippocampus has also been included as part of the olfactory centers, and guided by the work of Edinger, Elliot Smith, Zuckerkandl and Ramón y Cajal, we now consider this as a tertiary center for olfactory receptions.

For a long time the tuberculum olfactorium (lobus parolfactorius), lying mesial to the lobus olfactorius, was also considered to belong to the same general olfactory apparatus, but latterly, especially through the work of Edinger, this has become very doubtful. He looks upon it as the center for a special sense, which he has termed the 'oral sense,' and which is especially large in those animals which have highly developed sense perceptions in the snout region.

In addition to the fibers joining the lobus pyriformis to the hippocampus (Edinger '11, p. 380) there arise from the olfactory and parolfactory lobes, several other bundles which join these structures to the tertiary centers. (1) The tractus olfacto-hippocampanicus is strongly developed in macrosmatic animals, especially where the corpus callosum is small or lacking, but it dwindles in man to the stria longitudinalis Lancisii. (2) The fasciculi parolfacto-hippocampo-septales, first described by Zuckerkandl ('87), pass into the septum pellucidum, and unite at the dorsal and caudal end of this structure with the fornix fibers. After this union they go back together and enter the cortex of the hippocampus. According to Edinger this is a very primitive

connection. (3) The taenia semicircularis, also, arises somewhere in the neighborhood of the base of the corpus striatum, probably mainly from the lobus parolfactorius, follows the boundary between the thalamus and the nucleus caudatus and ends, curving downwards and forwards, in the nucleus amygdalae. (4) The stria medullaris thalami (taenia thalami) too, ending in the median side of the thalamus in the ganglion habenulae, is usually thought to be part of the olfactory structures. Edinger's work, however, has made it very probable that it belongs not, or at least not only, to the olfactory apparatus, but to what he calls the parolfactory apparatus, whose center lies in the lobus parolfactorius.

The anterior commissure (commissura ventralis) is generally considered as the most important commissure of the olfactory apparatus. In its frontal bundle it contains fibers uniting the two olfactory bulbs, while its more caudal and dorsal bundle connects cortical parts which stand in some way related to the olfactory apparatus, viz., lobus pyriformis and subiculum. Also in many lower mammals where the hippocampus lies dorsad of the brain stem, and is not yet pushed back by the corpus callosum, there is a third bundle in the anterior commissure. Since Owen's work, and, more recently, by that of Elliot Smith and Symington, we know that this third part consists of a thick strand of fibers which runs to the dorsally placed hippocampus. Thus while in most mammals the commissura anterior has the form of a double horse-shoe lying in a horizontal plane, as is well shown in figure 290, page 386, of Edinger's Vorlesungen ('11), in monotremes and marsupials there is a third horse-shoe standing upright upon the connection of the other two, uniting the aforementioned dorsal cortical parts.

The other commissure of the olfactory apparatus is the psalterium (commissura dorsalis), which is made up of crossing fibers between the two hippocampi themselves.

Other structures which may be partly connected with this system are the claustrum, lying outside of the nucleus lentiformis and under the cortex; and (with more certainty in the lower vertebrates) the corpus striatum. Whether these should be included in mammals is quite doubtful.

According to Edinger and Wallenberg, there is a tract, the basal olfactory bundle, running from the olfactory bulbs and peduncles in a direct path to the region of the corpora mamillaria, and part of the fibers may go even to the ganglion interpedunculare.

These parts of the mammalian brain, which are concerned in the conduction of olfactory and associated impulses vary greatly in their form and position, and in their size relative to surrounding structures, in the different species. This variation depends upon two main circumstances. The first is the degree of development of the olfactory mechanism itself. The second is the position that the animal has attained in the scale of intelligence, this being connected, usually, with the size of the neopallium. In the higher forms, there is increasing development of the neopallium, and consequent overshadowing of the primitive parts.

As the lower orders of mammals possess, in general, a well-developed olfactory sense, without any great development of the neopallium, they present a more easily understood olfactory mechanism. The study of such forms in recent years has made clear the fundamental olfactory portions of the brain. With the increasing development of the neopallium and associated structures (frontal and temporal lobes, corpus callosum) and often the decreasing importance of the olfactory structures, a much more intricate arrangement has been arrived at, as in the human brain. An intermediate condition, where there is a medium development, both of the olfactory apparatus and of the neopallium, is found in many animals, such as terrestrial Carnivora and the ungulates.

These three grades are illustrated in figures 1, 2, and 3, in the drawings of the base of the brain of the rabbit, calf and man. These demonstrate the external differences between macrosmatic and microsmatic forms, and the variation which may exist in the relative extent of the rhinencephalon within the macrosmatics.

Partly perhaps as the result of this morphological variability, one often finds a diversity of meaning attached to one term, as used by the various investigators working on comparative

and human brain anatomy. In the description of the figures as given below, I have followed closely the nomenclature used by Beccari ('10, '11), who studied in Edinger's laboratory.

The regio olfactoria (olfactory lobe) is seen in figures 1, 2 and 3, to consist of bulbus olfactorius (which receives the processes

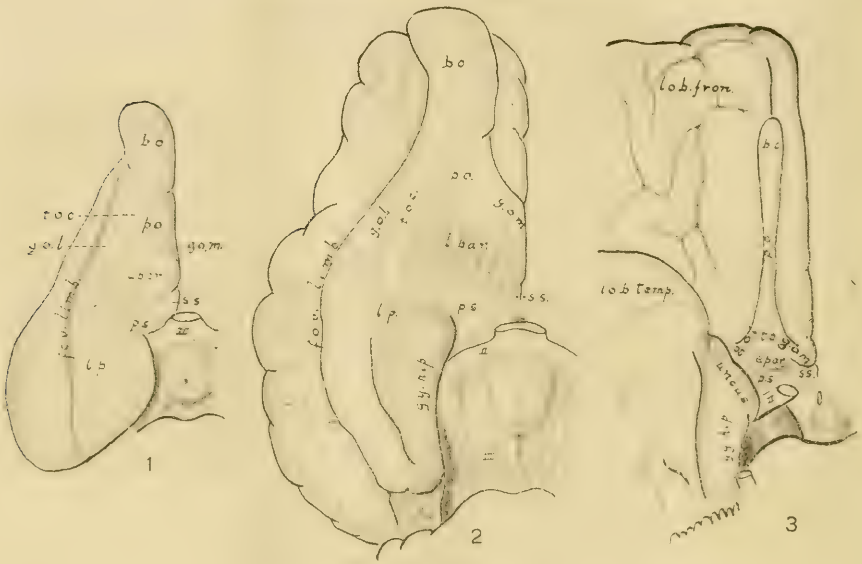


Fig. 1 Base of brain of rabbit (Lepus cuniculus), a macrosmatic animal with small pallium. Shows great development of olfactory and parolfactory structures. These extend the entire length of the brain, and include all parts designated by letters, mesial to the fovea limbica. $\times 1\frac{1}{2}$.

Fig. 2 Base of brain of calf (Bos taurus), a moderately macrosmatic animal, with increased size of neopallium. The parts of the cerebrum mesial to the fovea limbica, and anterior to and including the region marked *l.p.*, belong to the palaeencephalon, and are all olfactory and parolfactory structures. The remaining parts of the cerebrum shown are neencephalic. The lobus pyriformis is much reduced and ends by merging with the uncus of the gyrus hippocampus. The increased size of the neopallium is better seen from the lateral aspect. $\times \frac{3}{4}$.

Fig. 3 Portion of base of adult human brain, microsmatic and having great development of neopallium. The olfactory bulb is small, and the peduncle is much elongated. The eminentia parolfactoria is small, or may be nearly wanting. The remains of the lobus pyriformis are within the vallecula Sylvii, and have become overgrown by and fused with the temporal lobe. The extent of the lobus pyriformis is more distinctly seen in the brain of the 5-month fetus. $\times \frac{3}{4}$.

of the olfactory cells), pedunculus olfactorius, tractus olfacto-corticalis (figs. 1 and 2), medial and lateral olfactory gyri, and lobus pyriformis (figs. 1 and 2). The regio parolfactoria comprises the lobus parolfactorius (in man, preferably called eminentia parolfactoria), the planum septale and stylus septi. The planum septale is Beccari's term for the anterior perforated space of human anatomy, while the stylus septi comprises two structures—the diagonal band of Broca (*bandelette diagonale*), and the gyrus subcallosus of Zuckerkandl. In the microsmatic human brain, having great pallial development, the bulbus is extremely

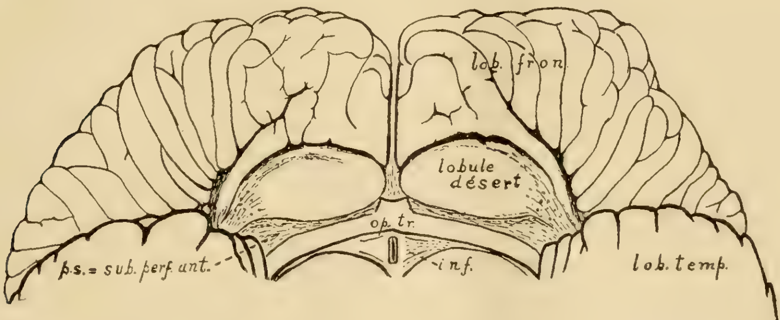


Fig. 4 Anterior portion of base of brain of dolphin, anosmatic and with large and highly convoluted pallium. Shows lack of external olfactory structures and presence of a conspicuous oval field on each side, *lobule désert*, where the cortex is lacking, and the head of the corpus striatum comes to the surface. Very distinct furrows marked off the *lobule désert* in this brain. × $\frac{4}{5}$.

ABBREVIATIONS

FIGURES 1 TO 4

b.o., olfactory bulb
e.par., eminentia parolfactoria (fig. 3)
fov.limb., fovea limbica, or ectorhinal fissure
g.o.l., lateral olfactory gyrus
g.o.m., mesial olfactory gyrus
gy.hip., gyrus hippocampus
inf., infundibulum
l.p., lobus pyriformis
l.par., lobus parolfactorius (= eminentia parolfactoria, fig. 3)
lob.fron., frontal lobe
lob.temp., temporal lobe
lobule désert, or désert olfactif, Broca
op.tr., optic tracts
p.o., pedunculus olfactorius (or olfactory tract, fig. 3)
p.s., planum septale (*piano settale*) or anterior perforated space
s.s., stylus septi
t.o.c., tractus olfacto-corticalis

small, and the olfactory peduncle or tract narrow but very elongated. As Elliot Smith ('02) points out, the length of the peduncle in the human brain is probably brought about by the bulb being anchored in a fixed position by the olfactory nerves coming through the cribriform plate, and by the increase in size of the frontal lobe, which moves backward the position of the attachment of the peduncle to the base of the brain. These two circumstances result in the great attenuation of the peduncle.

The lobus parolfactorius in the calf (fig. 2) shows an appearance typical for many macrosmatic animals, as found by Beccari ('10). In man this region is so reduced as to make the term eminentia parolfactoria more appropriate. According to Beccari ('11) who investigated a series of fifty human brains, in twenty-five per cent (25%) it was well developed, in fifty per cent (50%) weakly developed, and in twenty-five per cent (25%) was lacking. This region has been the subject of recent controversy. Edinger has wished to separate it from the olfactory system, and asserts that but few olfactory fibers (e.g. of tractus olfacto-corticalis) penetrate it, but that it receives tracts from the region where the trigeminus ends. The lobus parolfactorius he would designate as the center for impulses, coming by way of the fifth nerve, from specialized sensory structures in the snout region. Its variation in size in the different species he would correlate not with the olfactory sense but with the 'oral sense,' the height of development of which depends upon the size and character of the innervated area at the oral pole. Elliot Smith, using the brain of Orycteropus, contended that many fibers of the olfactory tracts could be seen covering and entering this lobe and hence that it should still be called tuberculum olfactorium. Later Edinger studied sections of the brain of Orycteropus and found that this lobe received none or very few of the olfactory fibers. The region was examined carefully by Beccari ('10, '11) in a series of mammals and in man, and he agrees with Edinger that it is a special field, but does not think the proof quite sufficient that it has to do with an oral sense. He found that it has well developed connections with the hippocampus, nucleus amygdalae, and ganglion habenulae, slighter

with the regio olfactoria, and perhaps some with the nucleus of the fifth nerve. Bindewald ('13) studying this region in the elephant, found it very large as one might expect in an animal with such a large and sensitive snout apparatus as the trunk. Thus there is no final agreement as to its status at the present time.

The planum septale, or anterior perforated space of human anatomy, is a region where normally the central ganglia come to the surface without any cortical covering. In the dolphin (fig. 4) we will see that there is a much increased area of central ganglion exposed.

The extent of the lobus pyriformis varies greatly in different orders, but in all it is a palaeencephalic structure. In lower mammals it comprises the entire region mesial to the fovea limbica or rhinal fissure, but in higher mammals neopallial structures also develop in this area. In this view of the adult human brain (fig. 3), practically nothing is seen of the much diminished lobus pyriformis within the vallecula Sylvii, but in the 5-month fetus brain it is easily recognizable as an acutely bent band running laterad of the planum septale, and ending caudally in the temporal lobe (see Villiger-Piersol, 1912, p. 26, fig. 26). In the adult this caudal portion becomes fused with part of the temporal lobe, although the diminutive gyri semilunaris and ambiens still show as landmarks indicating its limit, and the slight incisura temporalis at the margin of the uncus persists as the representative of the primitive rhinal fissure.

EXTERNAL FORM OF DOLPHIN BRAIN

The cetacean brain is wide and blunt, and presents an appearance quite different in some respects from that of all other mammals (figs. 4 and 6). The frontal part does not taper towards the nose, but curves round in a strange way, so that what is usually the most frontal point has to be looked for at the base of the brain, not far frontad of the chiasma. Thus the whole organ is not egg-like in form but is more globular, and it is quite possible that this shape is the result of the retrogression of its olfactory

system. This was the opinion of Tiedemann ('26) and also of Elliot Smith ('02), but another explanation may be offered.

The fact that, in the process of adjustment of the organism to the new environment, the external respiratory opening has come to open at the dorsal surface of the head in these animals, instead of at the extremity of the snout, may also be a factor in limiting the growth of the brain anteriorly. When one examines the cranium, the air-chambers are seen to descend directly in front of the cranial cavity. In an animal which must come to the surface to breathe every few seconds, it is evidently convenient to have the air-openings on the dorsal surface of the head, and equally desirable that the pathway to the pharynx and larynx should be most direct, and this is certainly helped by the shortness anteriorly of the brain-box. Thus there may be a correlation between the change in position and direction in the air-passages, and the peculiar shape of the brain, entirely apart from the presence or absence of olfactory structures in the brain.

In the Mystacoceti (baleen whales) there is a diminutive olfactory bulb and peduncle, but in some of the Odontoceti (toothed whales) these structures are wanting. This is the case in the adult dolphin, where there is not the slightest trace of olfactory nerves, even in microscopic sections. In Globiocephalus melas there is reported to be complete absence of external olfactory structures in the brain by Pettit ('05), and this is the condition, too, in Beluga (Delphinapterus) according to Kükenthal and Ziehen ('89), who state, also, that there is a slight development of the olfactory structures in the embryo. In Tursiops truncatus, specimens of which lived for some time in the New York Aquarium, no olfactory bulbs and tracts were seen when the brains were removed in the laboratory of Prof. G. S. Huntington. Although Delphinus is destitute of olfactory nerves, others of the family Delphinidae possess them. Thus, in Phocaena (Edinger '11) there is a microscopic trace of these structures, and in Hyperoodon of the family Platanistidae there are also small olfactory nerves (Kükenthal and Ziehen, '89). Thus among the toothed whales, some have small olfactory structures while others have none at all.

Early observers who pictured cetacean brains which exhibited absence of olfactory structures were Tiedemann ('26) and Stannius ('46).

The outside form of these cetacean brains is known from the works of several writers, the furrows especially having been discussed by Kükenthal and Ziehen ('89) and Elliot Smith ('02), among others. But sections have only twice been studied. In 1905, at the Baden Congress, Jelgersma read a paper on the results of his study of the brain of Phocaena, but this has never been published except by title. And also we have a very good description of the brain-stem of Delphinus by Hatschek and Schlesinger ('02), in which, however, the study of the forebrain and olfactory apparatus was outside of the special plan of their work.

EXTERNAL OLFACTORY REGION

The ventral surface of the dolphin's brain (figs. 4 and 5) gives at first the impression that, though the olfactory tract and lobe are entirely absent, the lobus parolfactorius is still present in large size. One sees just in front of the chiasma, on either side, a large, somewhat oval, convex, protruding area, quite distinct in appearance from the substance of the frontal lobe. Broca, who was surprised to find no convolutions there, called it '*lobule désert*.' This lies at a place where one finds in other mammals the lobus parolfactorius, and indeed, like this, it has behind it a typical substantia perforata anterior, as already described by Kükenthal and Ziehen. Frontally it is separated from the cortex of the frontal lobe by a depression which shows considerable variation in extent and depth in the several brains examined. In one of the brains (fig. 4), it was very deep and showed as a continuous furrow. In another (fig. 5 A) the depression was quite shallow and as a result the area did not appear so bulging. In a third, depicted in figure 5 B, there was a distinct furrow mesially, but this became less marked laterally.

Laterally this area extends as a narrow grayish band, which disappears, getting narrower and narrower, in about the region where the nucleus amygdalae lies. This narrow grayish band

occupies the position which in macrosmatic mammals is occupied by the large olfactory lobe, and may be here the remnants of the atrophied olfactory lobe.

Stained sections show that the main part of the bulging out of Broca's '*lobule désert*' is made by the head of the nucleus caudatus which is at this place curved round to the ventral surface

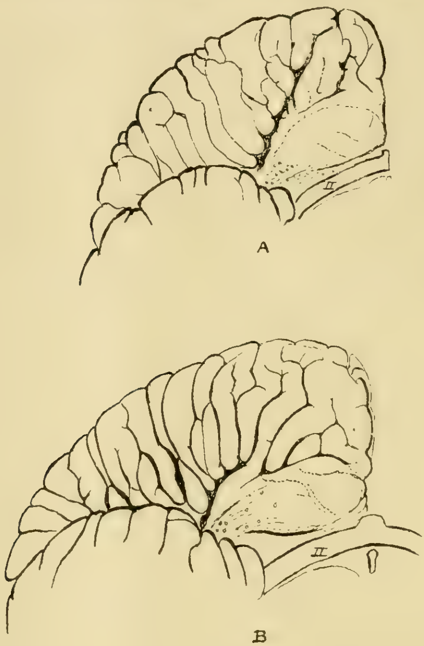


Fig. 5 Basal view of anterior portions of hemispheres of brains of two other dolphins, to show variations in depth of the depressions surrounding the *lobule désert*. In neither are the furrows so marked as in the brain shown in figure 4. In A, the furrow frontad of the *lobule désert* is very shallow, while in B, it shows as a distinct depression mesially, but nearly disappears laterally. $\times \frac{4}{5}$.

of the brain. But the protuberance is covered at its ventral surface by two sorts of cortex. Frontally and mesially there is a continuation of the typical frontal cortex, but caudally and everywhere laterally there is another cortex-like covering. Separating the one from the other are one or two shallow furrows, as shown in the figure of section 153 (fig. 11). The gray substance of the frontal cortex here shows the same general structure as

elsewhere. The other part of the cortical covering, divided from the frontal cortex by one or two shallow furrows, is made up of gray matter covered by a medullated nerve layer of very fine fibers. This layer of nerve fibers is pushed down here and there into little processes, which project into the underlying gray substance and thus give a somewhat undulated appearance to the outline of the latter.

Fig. 6 Median sagittal section of brain of adult dolphin. The numbered lines indicate the planes and positions of the sections which have been drawn. In comparison with brains of macrosmatic animals, it shows a rounded form in the frontal region, and not a tapering form. The floor of the central canal of the brain recurves, as it descends from the aqueduct of Sylvius to the posterior wall of the infundibulum. The corpus callosum is large and well-arched. The anterior commissure is very small. $\times \frac{4}{5}$.

It is more than probable that this slightly convoluted cortical-like plate, which lies just where we are accustomed to see the more distinctly convoluted cortex of the lobus parolfactorius, constitutes the last remnants of this formation.

Laterally (fig. 11) the medullated fibers are more numerous and more closely packed, so that the lateral aspect of the nucleus lentiformis is covered only by a relatively thin layer of grayish-

white substance which has not the aspect of any definite cortex-form. One is inclined to regard this part as being the last remnants of the olfactory lobe (fig. 11).

So one concludes that the main part of the bulging out of the base of the brain is made by the caput nuclei caudati. This is covered anteriorly and mesially by cortex of the frontal lobe. Laterally it is covered by the remnants of the olfactory lobe, and between these two is situated what remains of the better preserved, but still highly atrophied parolfactory cortex. It is also to be noted that the head of the striatum is separated from both varieties of cortical gray coverings by a thin layer of medullated nerve fibers.

More caudally (fig. 9), all three sorts of cortex—frontal, parolfactory and olfactory—disappear, leaving only a thin layer of white fibers over the otherwise naked protrusion of the caput nuclei caudati.

TERTIARY CENTERS AND CONNECTIONS

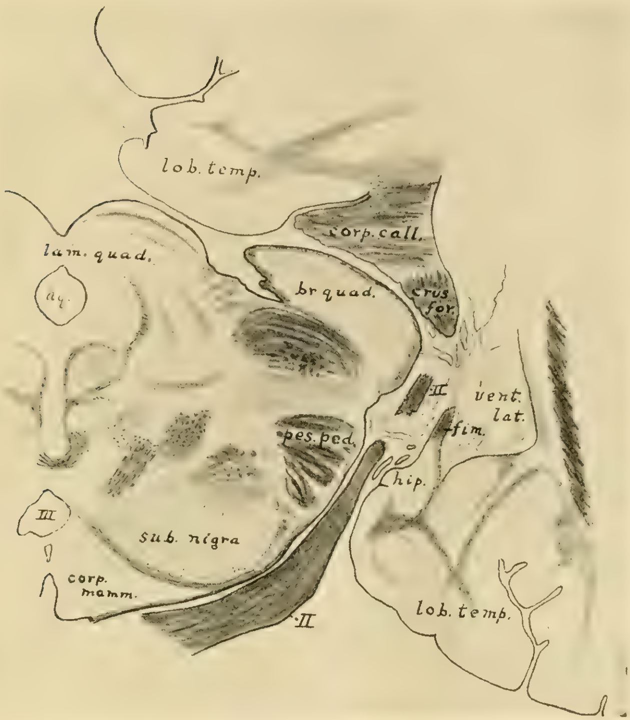
The hippocampus, as shown in its general relations (fig. 7) and in its detailed formation (fig. 8), is an extremely small atrophic structure and it is with some diffidence that one attempts to homologize its parts with those of even the microsmatic type of

Fig. 7 Ventral portion of section 125, as shown in figure 6. The brain-stem is cut nearly transversely, showing mid-brain for the most part, but also, ventrally, a small portion of the infundibular region. Laterally and dorsally are portions of the temporal lobes (*lob.temp.*). Forming the mesial wall of the lateral ventricle (*vent.lat.*), are the fimbria (*fim.*) and atrophic hippocampus (*hip.*). A caudal part of the corpus callosum (*corp.call.*) is seen laterally, and beneath it the beginning of a crus fornicis (*crus for.*). The continuity between the fimbria and fornix does not show at the level of this section. × 2.

II, optic tract; *III*, third ventricle; *aq.*, aqueduct of Sylvius; *br.quad.*, brachium quadrigeminum; *corp.mam.*; region of corpus mamillare; *lam.quad.*, quadrigeminal plate; *lob.temp.*, temporal lobe; *pes.ped.*, pes pedunculi; *sub.nigra*, substantia nigra.

Fig. 8 Detailed drawing of hippocampal region of preceding figure, showing small size of the constituent structures. The atrophic hippocampus shows no elevation within the lateral ventricle. Groups of large cells represent the gyrus dentatus (*gy.dent.*). The fissura hippocampi (*f.h.*) is extremely small, and below it, the region of the subiculum (*subic.*) is represented by the portion of the cortex containing fine medullated fibers. The nucleus amygdalae (*nuc.amyg.*) occupies a position in the floor of the lateral ventricle. × 5.

fimb., fimbria; *g.h.*, gyrus hippocampi; *plexus*, plexus in lateral ventricle.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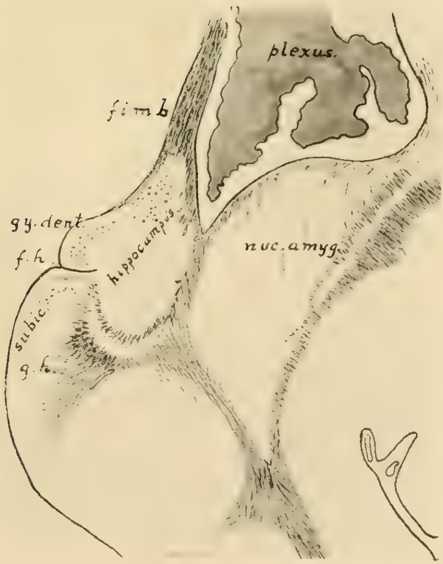
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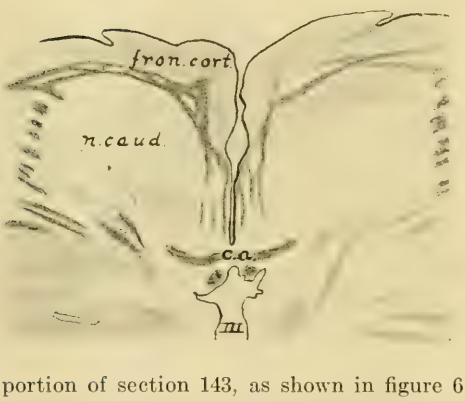

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Fig. 9 Anterior portion of section 143, as shown in figure 6. Anteriorly is shown the head of the caudate nucleus (*cap.n.caud.*) without any definite covering of cerebral cortex. In the temporal lobe (*lob.temp.*) is the nucleus amygdalae (*n.amyg.*), subdivided by crossing bundles of medullated fibers. Ventral to the corpus callosum (*corp.call.*) is a more lightly staining band of fibers, crossing the midline and constituting the psalterium (*psalt.*). The lateral regions of this band contain fibers which, not crossing, continue as the fornix fibers. × 2.

II, fibers of optic tract; *III*, third ventricle; *aq.*, aqueduct of Sylvius; *gy. cing.*, gyrus cinguli; *lam.quad.*, quadrigeminal plate; *thal. op.*, optic thalamus.

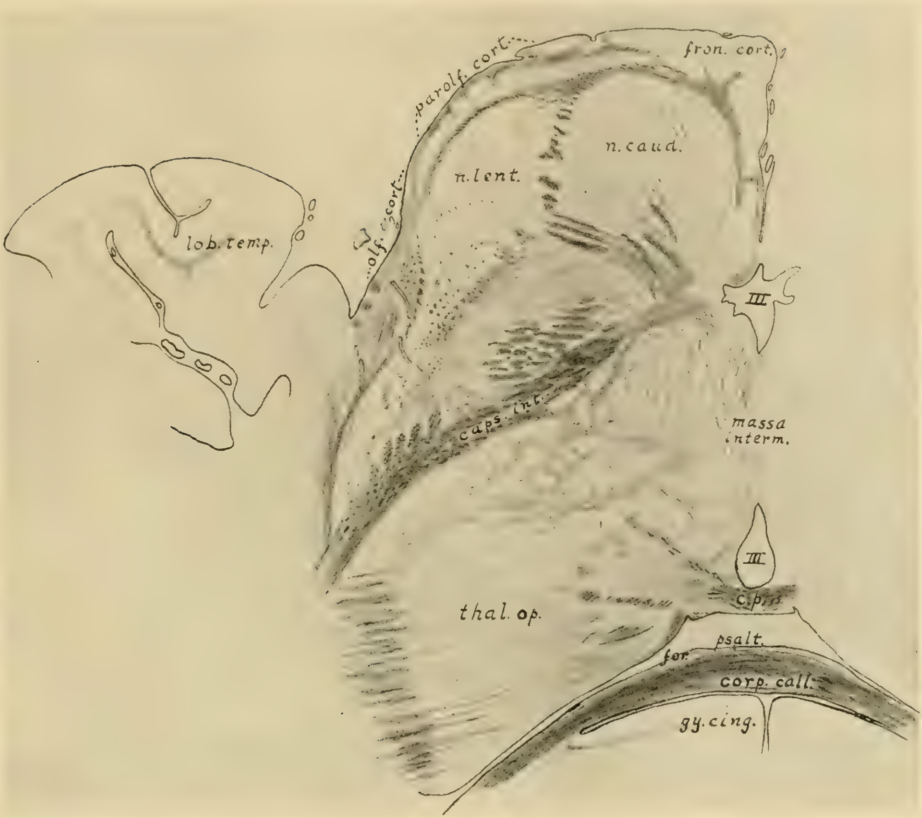

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Fig. 10 Anterior portion of section 148. Shows the anterior commissure (*c.a.*) as a very narrow strand, disappearing laterally in the caudate nucleus (*n.caud.*). $\times$ 2.

III, third ventricle; *fron.cort.*, frontal cortex.

Fig. 11 Anterior portion of section 153, as shown in figure 6. Covering the caudate nucleus (*n.caud.*) is the typical frontal cortex, but covering the nucleus lentiformis (*n.lent.*) are two differently-appearing surface coverings. The remains of the parolfactory cortex are shown by the presence of a superficial fiber layer, raised internally at intervals into little elevations. The region marked *olf.cort.*, is taken to be region where the olfactory cortex existed formerly. Ventral to the corpus callosum (*corp.call.*) is a more lightly staining band which contains fibers (1) of the psalterium (fibers crossing the midline), (2) of the fornix (*for.*) which are laterally placed, and (3) possibly of Zuckerkandl's bundle. $\times$ 2.

III, third ventricle; *caps.int.*, internal capsule; *c.p.*, posterior commissure; *gy.cing.*, gyrus cinguli; *lob.temp.*, temporal lobe; *massa interm.*, massa intermedia; *thal.op.*, optic thalamus.

hippocampus. As there were no cell-preparations available for study, one can say nothing of the cell-layers, but one can readily appreciate the simple atypical form of the hippocampus, and its small size, which produces no apparent bulging into the ventricle. There is a very shallow fissura hippocampi, below which, in figure 8, there is seen a small cortical area of the gyrus hippocampi, containing superficially a layer of fine medullated nerve fibers. This small cortical area is evidently the representative of the subiculum. There is no separated gyrus dentatus but above the fissura hippocampi are clusters of cells, which may represent the remnants of the gyrus dentatus. At the apex of the whole formation proceeds the fimbria in the typical way. Descriptions of the outer appearance of the hippocampus are to be found in Broca ('79), Zuckerkandl ('87) and Elliot Smith ('02).

The fimbria arises as a narrow elongated bundle from the margin of the hippocampus (figs. 7 and 8). Part of its fibers cross soon to the opposite side forming the hippocampal commissure, commissura dorsalis, or psalterium. This is shown as a rather broad band of fibers in figure 9, lying ventral to the corpus callosum, and consisting of fibers which stain more lightly than those of the corpus callosum. The psalterium appears so well developed that the possibility is suggested that it may contain other fibers in addition to the commissural hippocampal fibers. Perhaps fibers coming from the parolfactory cortex may cross here to reach the opposite hippocampus. A small portion of the psalterium is still apparent in section 153 (fig. 11). Other fibers of the fimbria proceed uncrossed as two flattened bands of the crura fornicis (section 169, fig. 12). These approach one another in the midline (section 181, fig. 13), where they form the body of the fornix. The general course of the fornix fibers is shown in figure 15, as reconstructed from several consecutive sagittal sections. The fornix fibers proceed under the corpus callosum until they enter the margin of the septum pellucidum (figs. 13 and 14). They traverse its curved outline and so are cut across twice in figure 13. They are seen again in figure 12, in the most anterior and ventral portion of the septum pellucidum. In our series of sections cut as shown in figure 6, we were unable

to follow these farther with certainty and so were of the opinion that all these fibers ended near this point, perhaps in the parolfactory cortex, and belonged to Zuckerkandl's bundle. But later Professor Edinger has been able to study a sagittal series, and finds that these fibers, or most of them, curve round in the

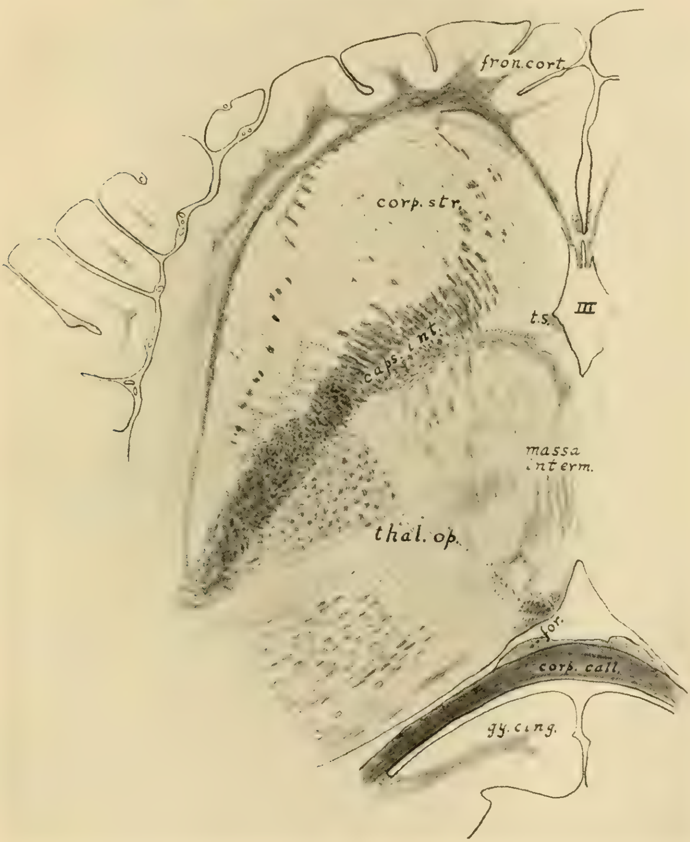

Fig. 12 Anterior portion of section 169, as shown in figure 6. The corpus striatum (*corp.str.*) is here covered by typical frontal cortex (*fron.cort.*). The taenia semicircularis (*t.s.*) is seen in the groove between optic thalamus (*thal.op.*) and corpus striatum (*corp.str.*). The massa intermedia (*massa interm.*) is cut across it greatest diameter. Ventral to the corpus callosum (*corp.call.*) are seen the two strands of the fornix (*for.*). × 2.

III, third ventricle; *caps. int.*, internal capsule; *gy.cing.*, gyrus cinguli.

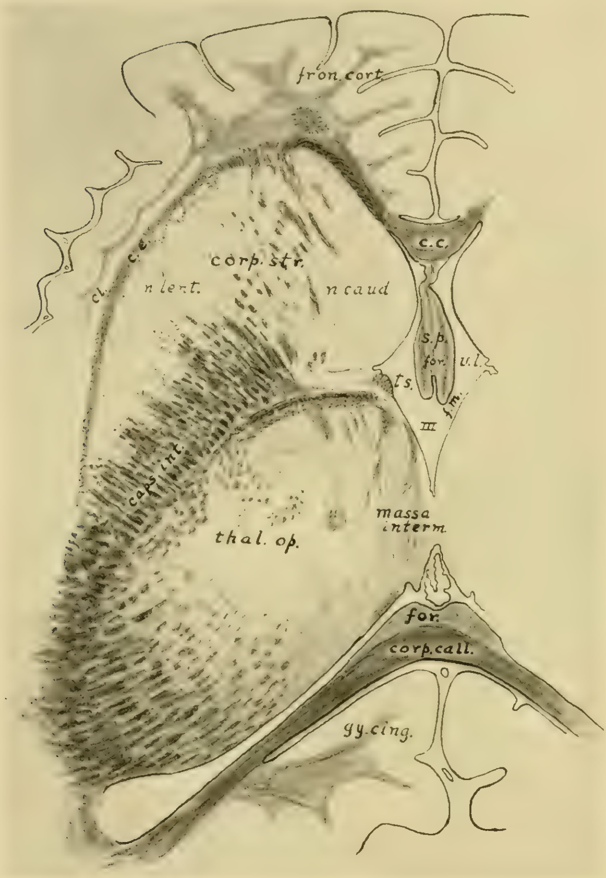

Fig.13 Anterior portion of section 181, as shown in figure 6. Shows the corpus callosum and fornix cut through twice. Beneath the more caudal part of the corpus callosum (*corp.call.*) the body of the fornix (*for.*) is seen as a flattened band. The fornix is again cut in the septum pellucidum (*s.p.*) near its free margin. The taenia semicircularis (*t.s.*) is seen in the groove between caudate nucleus (*n.caud.*) and optic thalamus (*thal.op.*). The massa intermedia (*massa interm.*) is cut through its most frontal portion. × 2.

c.e., external capsule; *caps.int.*, internal capsule; *cl.*, claustrum; *corp.str.*, corpus striatum; *f.m.*, foramen of Monro; *fron.cort.*, frontal cortex; *gy.cing.*, gyrus cinguli; *n.lent.*, nucleus lentiformis; *v.l.*, lateral ventricle.

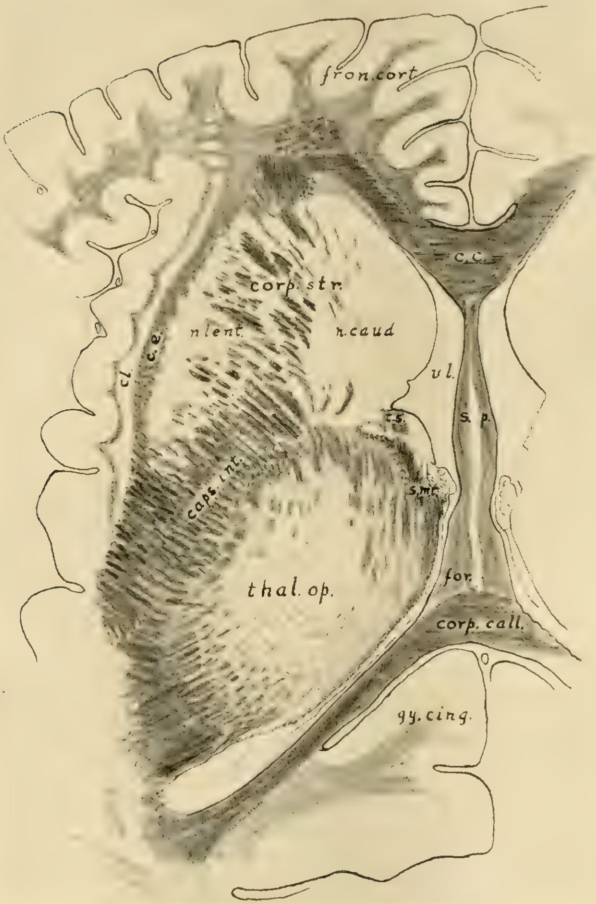

Fig. 14 Anterior portion of section 186, as shown in figure 6. Shows corpus callosum cut through twice (*c.c.*, and *corp.call.*) and the thin intervening septum pellucidum (*s.p.*). This is thickened at one region by the fornix fibers (*for.*). The taenia semicircularis (*t.s.*) is in the groove at the junction of the corpus striatum (*corp.str.*) and the optic thalamus (*thal.op.*). On the margin of the latter are the fibers of the stria medullaris thalami (*s.m.t.*). × 2.

c.e., external capsule; *caps.int.*, internal capsule; *cl.*, claustrum; *fron.cort.*, frontal cortex; *gy.cing.*, gyrus cinguli; *n.caud.*, nucleus caudatus; *n.lent.*, nucleus lentiformis; *v.l.*, lateral ventricle.

typical fornix fashion to the infundibular region, probably ending as usual in the nuclei of the corpora mamillaria.

The corpora mamillaria are very slightly developed, and do not show as typical rounded protuberances. However, immediately caudad of the posterior wall of the infundibulum is a median fissure (fig. 7, section 125), separating gray substance on either side which may be taken to represent the position of the two corpora mamillaria. In the series studied, there were practically no medullated fibers detected in these gray masses, but as the fornix fibers penetrate here, there must be some medullated fibers present.

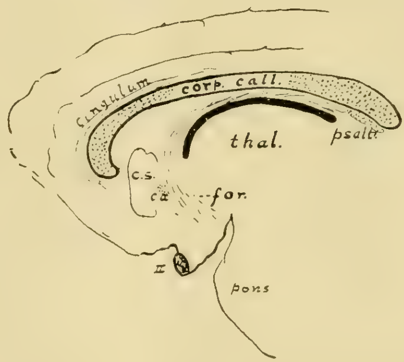

Fig. 15 Diagram of course of fornix fibers, reconstructed from several consecutive sagittal sections (after drawing sent by Professor Edinger).

II, optic nerve; *c.a.*, commissura anterior; *c.s.*, corpus striatum; *corp.call.*, corpus callosum; *for.*, fornix.; *psalt.*, psalterium; *thal.*, thalamus.

The taenia thalami or stria medullaris thalami is present as a very thin flat bundle lying in the usual position at the mesial ridge of the thalamus opticus (fig. 14, section 186). Followed anteriorly it becomes thinner and thinner, and cannot definitely be traced to the region where it begins, viz., in the parolfactory and olfactory cortex. Followed posteriorly towards the ganglion habenulae the number of fibers apparently increases, being augmented probably by fibers orginating in the stratum zonale thalami. It is quite possible that the olfactory and parolfactory portions are entirely absent.

The taenia semicircularis is shown in figures 12, 13, and 14, lying in the groove between the thalamus and the caudate nucleus, and also in figures 11 and 10 as it approaches its origin. Its fibers arise probably in the same region as that of the olfactory and parolfactory part of the taenia thalami but in these sections this was equally difficult to see. Its termination, the ganglion amygdalae, however, is well developed as illustrated in figure 9, section 143, which cuts its greatest expansion, and in figure 8, section 125. It is situated at the extremity of the lateral ventricle in the temporal lobe, and lies partly in the ventricular floor (fig. 8). It shows its typical appearance, several medullated tracts traversing it and dividing it into smaller nuclei. The ganglion cells did not appear to be the same size in all the compartments. In section 143, figure 9, the nucleus amygdalae is directly continuous with the cortex of the temporal lobe, but more caudally (section 126, fig. 8), where the nucleus is smaller, there is a layer of cortical white matter forming a line of separation between the nucleus amygdalae and the cortex. Here it bulges in the floor of the lateral ventricle as it lies laterad of the hippocampus.

The anterior commissure (fig. 10, section 148) is present as a small transverse bundle, which soon disappears when followed away from the midline. It is probable that of the two parts which usually make up the anterior commissure, only the posterior part is present, and that the anterior part connecting the olfactory bulbs is entirely absent.

SUMMARY

In the adult dolphin, the olfactory bulbs and tracts are lacking, and that portion of the mesethmoid which corresponds to the cribriform plate of the ethmoid of the ordinary mammal is imperforate. Hence the dolphin is completely anosmatic in the sense of Turner's classification.

In addition to the lack of olfactory bulbs and tracts, the olfactory cortex of the basal surface of the frontal lobe is also wanting. In consequence of the recession of the cortex in this region,

the corpus striatum of each side forms the surface as a convex oval area, the *lobule désert* or *désert olfactif* of Broca. The parolfactory cortex is also much reduced, but at least some definite remains of it are seen. This is interesting in the light of Edinger's view, that the tuberculum olfactorium is not a part of the olfactory system, but is the end-station of tracts conveying impulses by way of the fifth nerve from specialized sensory structures in the snout region. To the sense, which this mechanism serves, he has given the name 'oral sense.'

Of the several connections of the olfactory and parolfactory cortical cells with the hippocampus, none were seen with certainty. It is possible that from the parolfactory cortex some fibers of the fasciculi parolfacto-hippocampo-septales (Zuckerkandl's bundle) are still retained, but as the origin as seen in these sections was doubtful, and as they normally pursue most of their course with the fornix fibers, one cannot decide definitely from the material at hand.

Of the other possible connections of the olfactory and parolfactory cortical cells, both the stria medullaris thalami (taenia thalami) and the taenia semicircularis are seen, as are their respective end-stations the ganglion habenulae and nucleus amygdalae. The latter are both quite definite.

The hippocampi are very degenerate small structures, and it is with difficulty that one sees the analogy with even the microsmatic type of hippocampus. The fissura hippocampi is shallow but definite and the subiculum is present. The gyrus dentatus does not appear as a separate structure, but there are cell-groups which evidently indicate the position of what remains of it. Connected with the hippocampus is the fimbria, seen as a slender band of fibers. True fornix fibers are seen, and can be followed in sagittal series of sections When I reported, in a preliminary way, at the meeting of the American Association of Anatomists in December, 1914 (Anatomical Record, vol. 9, no. 1) this was not known to me, but this information has been kindly transmitted by Professor Edinger since that time. The corpora mamillaria where the fornix fibers end are greatly reduced in size. The psalterium or commissura dorsalis, formed of cross-

ing fibers between the two hippocampi is present very distinctly, but the anterior commissure is quite minute and it is probable that the olfactory portion is entirely lacking. The septum pellucidum is very thin.

Thus, this study of the brain of the dolphin shows that great atrophy of the hippocampal formation accompanies loss of the external olfactory structures, and that practically all the connecting tracts are likewise suppressed. The fact that both nucleus amygdalae and ganglion habenulae are present, though somewhat reduced, points to their having only a partial connection with the olfactory mechanism. There is a slight persistence of the parolfactory cortex, probably sufficient to give rise to, at least part of, the fibers of the stria medullaris thalami and taenia semicircularis.

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THE TROPHOSPONGIUM OF THE NERVE CELL OF THE CRAYFISH (CAMBARUS)

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ELEVEN FIGURES

Attempts to solve recognized cytological problems are continuously bringing new problems to the attention of the investigator. Improved instruments and new technique serve to bring to view unsuspected elements of structure in the constitution of the cell. The multiplication of physiological problems keeps pace with the increase of the morphological.

In cells of different tissues from various animals, both chordate and non-chordate, a more or less complex framework extends from without into the cell body. This is known as the trophospongium of Holmgren, or simply the trophospongium. Coghill in his review ('04) states that the first observation of such a structure in the nerve cell was recorded by Fritsch in 1886 in a study upon the medulla oblongata of Lophius; that Holmgren in 1899, in a report upon an investigation of the spinal ganglion cell of Lophius was probably the first to confirm this observation of Fritsch and that in the same year, 1899, Nelis described structures that evidently are the same as those observed by Fritsch and Holmgren. Since that date numbers of investigators have studied the trophospongium in its morphological and physiological aspects.

The descriptions of the trophospongium as given by some authors seem to indicate that the structure is composed of a reticulation of delicate fibers. On the other hand the description as given by Antoni refers to the capsular buds ('kapsuläre Sprossungen') from the intercellular tissue, that separate the protoplasm of the nerve cell into unequal lobes. These processes

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anastomose and not infrequently contain nuclei. Antoni evidently does not consider the trophospongium as a reticulation of fibers but rather as an anastomosis of partition-like walls. Holmgren evidently has the same conception of the structure as that given by Antoni.

There seems to be a practical agreement of opinion among investigators that the trophospongic material is fibrous in its general character and that it originates from glia or other non-nervous cells; but while some hold it to be of fibrous walls others evidently think it a reticulation of threads. Nuclei and blood capillaries have been observed in the trophospongium by different investigators.

Quite early the question arose concerning the relationship between the trophospongium of Holmgren and the internal reticular apparatus of Golgi. Holmgren's opinion that the structures are identical, by many investigators, is believed to be without justification. Holmgren believes he has good ground for the opinion that the canals for the conveyance of nutrients in the cell body ('Saftkanälchen') and the Golgi apparatus are identical and that the 'Saftkanälchen' are developments by a dissolution process of the trophospongium. In a recent paper, 1914, he upholds the opinion he has maintained for more than ten years. Further, Holmgren is of the opinion that the tracheal capillaries of the insect cell are identical with the trophospongium and the Golgi apparatus. In his interpretation of the relationship between the trophospongium and the Golgi apparatus Holmgren does not have many supporters. A number of investigators share the opinion that the theory is untenable, and express a belief in the distinct individuality of the two structures.

After the study of sections of quite a number of nerve cells from the grasshopper and cockroach, it is my opinion there is not much probability of any relationship between the trophospongium and the tracheal capillaries of the insect. The capillaries penetrate some of the nerve cells of the insect as delicate tubes which are direct continuations of the tracheae invaginated from the ectoderm during embryological development. The

capillaries become so small, one-half micron or less in diameter, that the supporting chitinous spirals or taenidia are absent. There is no morphologic resemblance to the trophospongium which is present in the grasshopper and cockroach cells, although not so strongly developed in these insects as in the crayfish.

The nerve cells of the abdominal ganglia of the crayfish, Cambarus, afford excellent material for the study of the trophospongium, as some of the motor cells are large and the trophospongium well developed. The ganglia may be fixed and stained by Bensley's acetic-osmic-bichromate acid fuchsin method, or fixed in Zenker's fluid and stained with Mallory's connective tissue stain. Other methods will doubtless give good results also. It is not necessary to use perfectly fresh tissue, as good results were obtained with ganglia from animals dead several hours. Both large and small cells contain the trophospongium, although it is more strongly developed and more prominent in the large cells and was not observed in many of the smaller. Nor does it show in equal degree in all the large cells, due in part possibly to a difference in response of the cells to the technique. The examination of serial sections, 4 micra in thickness, shows that the structure is not a reticulation of fibers but is an anastomosis of partition walls or of capsules extending into the cytoplasmic mass and dividing it into irregular lobes differing both in shape and in size. The cytoplasmic mass is continuous, however, as the lobes are only partially separated one from another by the incomplete partition walls. Some of the lobes are broad and flattened while others are somewhat conical or cylindric in outline. The trophospongium in some instances, as seen in sections, appears as a relatively low ridge rather broad at the base and giving off short, delicate branches near the free margin. In other sections, approaching the tangential sections, the ridges extend across the section, not infrequently almost parallel and connected by means of cross partitions. Near the center of the cell some sections show the structure extending into the vicinity of the nucleus, apparently as delicate fibrillae. The study of serial sections gives a conception of the trophospongium

altogether different from that obtained by the observation of a single section. Figure 10 shows a section of a motor cell of a crayfish that had been dead several hours before fixation of the tissue. Some peripheral vacuolation is evident. The trophospongium appears in section as fibers extending into the cell body. Figure 11 is of a section of the same cell between the center and the periphery. This shows in cross section some of the capsular processes that divide the cytoplasm into irregular lobes. Figures 1 to 9 show photomicrographs of nine sections of one cell. In these the anastomosing walls and the capsules are very evident. The sections are 4 micra in thickness Figure 1 is of the third section from the periphery, figure 2 of the fourth, figure 3 of the fifth, figure 4 of the eighth, figure 5 of the eleventh, figure 6 of the twelfth, figure 7 of the seventeenth, figure 8 of the twenty-third, and figure 9 of the twenty-fourth section. The total number of sections of the cell in the series is thirty-two. Others of the series would serve almost as well for illustration as those selected. A cursory examination shows the continuity of the trophospongium with the surrounding cell capsule. In figures 2 and 3, a nucleus is evident in one of the trophospongic walls at its connection with the cell capsule. This is the only nucleus observed in the trophospongium in the large number of sections studied. While some of the trophospongic walls are rather thick and heavy, the greater number are relatively thin and delicate, being only a few fibers in thickness. The continuity of the fibers with the cell capsule can be readily determined in sections 10 micra in thickness stained in Mallory's connective tissue stain following Zenker's fixation. Some of the fibers take on a red color, others blue.

R. Legendre suggests that the trophospongium is rarely present in the normal animal and that it may be characteristic of a pathologic condition. The suggestion is based upon his own observations, as he seldom found the structure in normal specimens but found it more abundant in the pathologic. This is not in accord with my observations upon the crayfish. In numerous sections from normal animals the trophospongium was found

to be well developed. Specimens exhausted in a water wheel did not show any stronger development, nor did one that was more or less under the influence of chloretone for two days. The sections illustrated in figures 1 to 9 were made from a cell of an animal apparently perfectly normal. Because of the presence of the structure in the crayfish nerve cells in normal and in abnormal conditions it is evident that in all probability the trophospongium is a permanent structure, not a transitory.

No very positive opinion concerning the function of the trophospongium has been expressed. The presence of blood capillaries as observed by Holmgren in Lophius logically indicates the possibility of a nutritive function. Theoretically a nutritive function is possible even in the absence of blood capillaries, as the trophospongium increases the capsular surface in contact with the cytoplasm thereby increasing the area of the osmotic surface. The absence of capillaries in the crayfish does not of necessity preclude the possibility of such a function. Several authors suggest that this is the function of the trophospongium. Logically there is a correlation between the morphology and the physiology of an organ. The crayfish nerve cell shows the development of the trophospongium into a structure admirably fitted for mechanical support. The anastomosing walls and capsules divide the cytoplasm into many lobes and offer substantial support to them. The smaller cells with an area proportionally greater in contact with the cell capsule do not have the trophospongium as strongly developed. The idea of a supporting function has been expressed by some authors, as Legendre and Gariaeff. It is not unreasonable to suppose that the structure functionates primarily as a mechanical support and secondarily as a nutritive organ.

SUMMARY

The trophospongium of the crayfish (Cambarus) motor nerve cell is well developed in normal animals.

It is non-nervous in character.

It is not identical with the Golgi canalicular apparatus, but is unrelated.

It consists of partitions and capsular processes continuous with the glia cell intercellular support, possessing nuclei only rarely.

Its structure is such that it affords mechanical support to the cytoplasm and possibly functionates in a nutritive capacity.

It is very similar to that of Lophius, indicating the probable identity of its origin in the chordata and non-chordata.

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EXPLANATION OF FIGURES

Figures 1 to 9, show a series of sections from a cell of a normal crayfish. Fig. 1, third section from periphery; fig. 2, the fourth; fig. 3, the fifth; fig. 4, the eighth; fig. 5, the eleventh; fig. 6, the twelfth; fig. 7, the seventeenth; fig. 8, the twenty-third; fig. 9, the twenty-fourth. Figures 1, 2, and 3 show the cross sections of contiguous lobes of the cytoplasm surrounded by the capsular trophospongium. Figures 2 and 3 show a nucleus, *n*, at the base of the trophospongic partition; this may in reality be a nucleus of the capsule rather than of the trophospongium. Figures 8 and 9 show a more pronounced flattening of the cytoplasmic lobes. Sections 4 micra, fixed and stained by Bensley's acetic-osmic-bichromate acid-fuchsin method. (Light splotches and dark cross, figures 5 and 7, are artefacts.) Zeiss 2 mm. obj., No. 2 ocular, magnification 500 diam., reduced to four-fifths in the plates.

c, canaliculi;
l, lobes of cytoplasm;
N, Nissl bodies;
n, nucleus;
tr., trophospongium.

Figures 10 and 11 were outlined with the Edinger apparatus with a magnification of 1000 diameters; reduced one-fourth in the half tone. Figure 10 is through the nucleus and shows intercellular nuclei in the capsule, trophospongium projecting into the outer zone of the cytoplasm, Nissl bodies, and canaliculi of Golgi. Figure 11 is of the same cell, the fifth section toward the periphery from Figure 10. In this the capsular character of the trophospongium is indicated, the capsular walls being transected. Sections 4 micra, from a crayfish dead several hours before being fixed and stained by Bensley's acetic-osmic-bichromate acid-fuchsin method.

Drawings and photomicrographs by the author.


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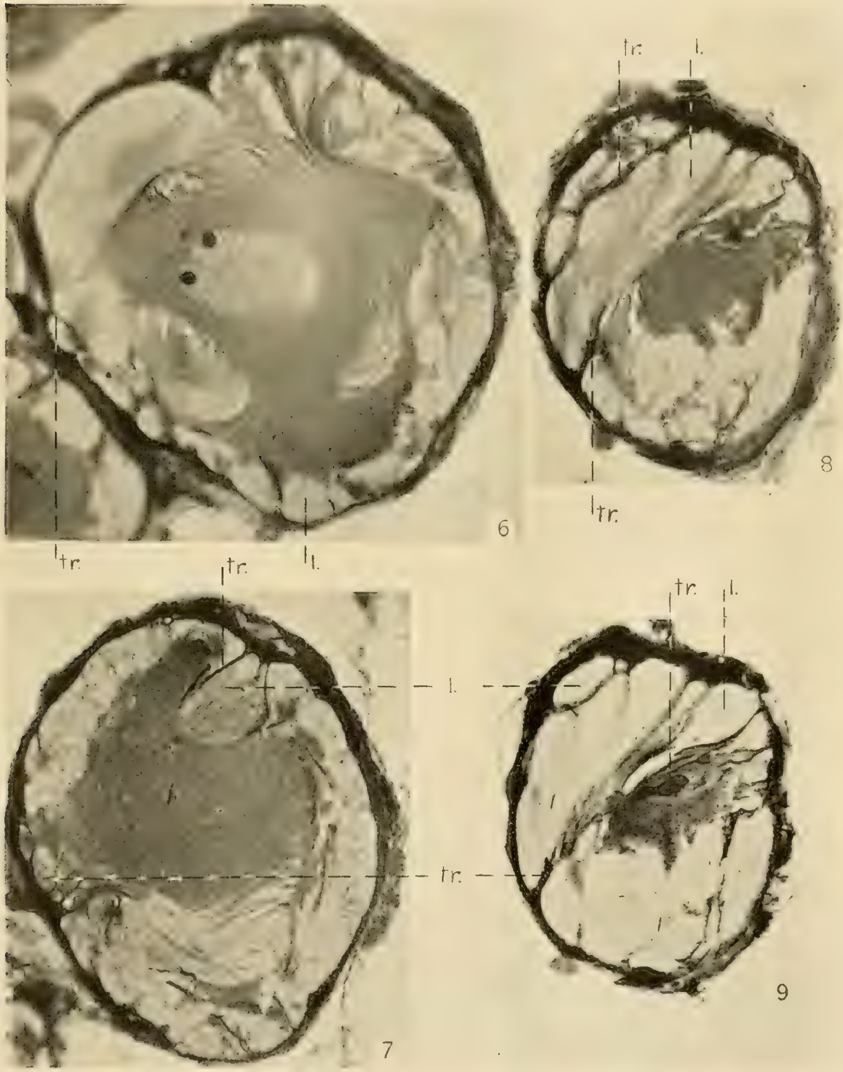
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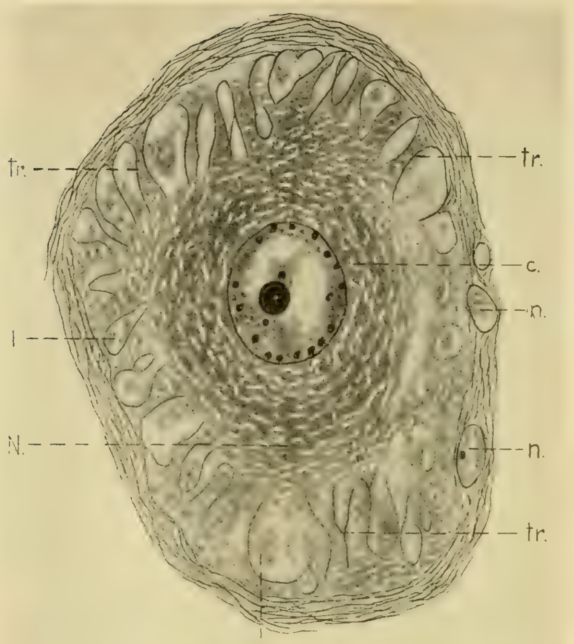

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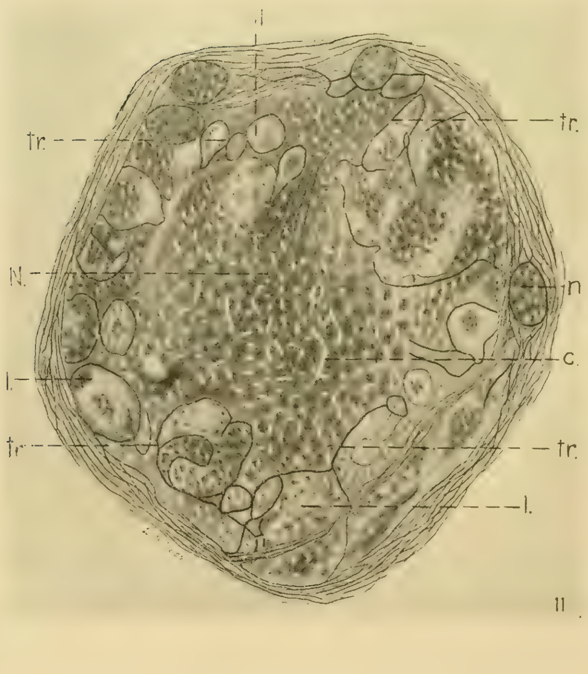

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CONTRIBUTIONS FROM THE ZOÖLOGICAL LABORATORY OF THE MUSEUM OF COMPARATIVE ZOÖLOGY AT HARVARD COLLEGE. NO. 264.

THE OCCURRENCE AND THE SIGNIFICANCE OF PHOTOMECHANICAL CHANGES IN THE VERTEBRATE RETINA—AN HISTORICAL SURVEY

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FOUR FIGURES

The exhaustive histological descriptions of the vertebrate retina published in the first half of the nineteenth century opened a field to physiological workers that has resulted in the production of many diverse investigations which, however, may be grouped into three general categories: 1) the physiology of the visual purple, 2) the action currents in the optic nerve, 3) the changes produced in the retina chiefly through the action of light. Of these three divisions the effect of light upon the retina has proven to be especially interesting and instructive, yet, strangely enough, this field has hitherto remained almost the exclusive property of the workers of continental Europe.

Stimulated by the results thus obtained among vertebrates, other investigators later undertook experimentation upon the invertebrate eye in order to discover whether similar conditions could be demonstrated among these animals. In the invertebrate types of eyes, however, due to the fundamental differences in structure, only partial agreement was to be expected.

A review of the literature dealing with the changes produced in the visual cells and retinal pigment through the action of light has never been presented in English, although an excellent compilation was published in 1907 by the German writer Garten. Since, however, Garten's review not only is of considerable length but also is inaccessible to many students, it has seemed desirable to present a brief summarization of the results that have been established by investigators in this field, together

with an account of certain theoretical considerations regarding the significance of these discoveries. No attempt will be made to trace the complete history of the investigations demonstrating the effect of light on the retinal elements, but only to outline the principal contributions that are of historical interest, as well as those that show the present status of the subject. In doing this, however, there will be included certain results that have escaped the attention of previous reviewers.

The rods, cones, and pigment in the retinas of many vertebrates undergo positional changes when adequately stimulated. A considerable number of investigators (since the first exact work by Mann '94) have also shown that changes occur in the bipolar and ganglionic cells of the retina through the influence of light. These workers, though often contradicting one another, have described changes in the shape and size of the retinal nuclei, and especially in the Nissl granules of the ganglionic cells, as due to the action of light. The occurrence of definite positional changes in these elements, however, has not been satisfactorily established.

For the sake of clearness it is preferable to trace separately the three lines of discovery which have demonstrated movements in the retinal pigment, in the cones, and in the rods. It should be remembered, however, that these three divisions are not historically isolated but are intimately connected through the overlapping results of many observers.

A variability in the degree to which the retinal pigment extended had been noted several years before the cause was suspected. Thus, H. Müller ('56) not only observed this variability but a'so saw that the pigment in many cases accumulated near the tips of the cones. Morano ('72) likewise questioned the constancy of the pigment distribution, stating that in some retinas the pigment extended only half the length of the outer member of the rods.

The first observation concerning the effect of light upon the retinal pigment was recorded by Czerny ('67), who, after concentrating sunlight on the retinas of various animals, found that the pigmented epithelium and the retina were less easily

separable in the blinded area. Examination showed the pigment in this region to be densely aggregated in processes which extended to the external limiting membrane, while in the remainder of the retina the pigment only reached to the inner members of the rods. Although these experiments were pathological, Czerny's statements show that he fully appreciated the potency of light in producing pigment migration.[1]

To Boll ('77) and Kühne ('77), working independently, belongs the credit of the first demonstration of the normal response of retinal pigment when stimulated by light. They established this fact conclusively by direct comparisons of light- and dark-adapted retinas of the frog, in which the pigment was observed to be highly expanded in the light but contracted in the dark (cf. figs. 1 and 2). Later observations have corroborated Kühne's original view that pigment migration is not due to the extension and retraction of cell processes, but to the movement of pigment granules in the protoplasm of relatively fixed cells.

Kühne's statement that a phototropic action on retinal pigment would be found in all vertebrates has not yet, in the case of most reptiles and mammals at least, been substantiated.

Among fishes and amphibians a response of the pigment to light seems general. Thus Stort ('86) on Perca, Pergens ('96) on Leuciscus, Hess ('02) on the marine eel, Exner und Januschke ('05) on Abramis, and Garten ('07) on the 'Weissfisch' have observed strong distal migration in the presence of light, while Kühne ('77) and Boll ('77) on the frog, Arcoleo ('90) on the toad,[2] and Angelucci ('78) and Stort ('86) on Triton found the existence of a similar condition.

The results on reptilian eyes, involving the query of Boll ('81) as to whether pigment migration occurs in rodless retinas, have been somewhat contradictory. Boll himself, working on the liz-

[1] Deutschmann ('82) repeated Czerny's experiment but did not find evidence of an extreme pigment migration. He says (p. 250)—"doch schienen zwischen den zerstörten Elementen der Stäbchenschicht mehr als gewöhnlich feine Pigmentkörchen zwischengelagert."

[2] Although Arcoleo experimented upon pithed toads only, striking responses were nevertheless obtained.

ard, and Angelucci ('78), on the lizard and turtle, both failed to find any influence due to the action of light, although Angelucci ('90) later demonstrated a rather limited pigment migration in the retina of Testudo marina, which has no rods. Chiarini ('06) reported that a distinct but limited pigment expansion was observed in the light-adapted eyes of the lizard. Finally, Garten ('07) found no significant differences in the light- and dark-adapted eyes of Lacerta, Emys, and the chamaeleon, although he admits that with strong illumination (as the dazzling Italian sunlight used by Chiarini) satisfactory preparations from Lacerta might be obtained.

In the retinas of birds, which usually possess both rods and cones, the pigment migration according to Chiarini ('06) is more pronounced than in reptiles. Stort ('87) showed this to be true both in areas of the pigeon's retina where rods are present, and to a more limited degree where they are absent. The influence of light was also observed in the hen (Krause '94), and in the owl (Angelucci '78), which are respectively diurnal and nocturnal in their habits.

The difficulty in obtaining preparations of the mammalian retina without separation of the pigmented epithelium and a coincident loss of pigment granules, renders exact judgments concerning the effect of light, very troublesome. The limited pigmentation of the retinas in this group increases the seriousness of faulty technique. Many investigators have regarded the adherence of the pigment to the retina as a criterion of the influence of light, yet this adherence, as Ewald und Kühne ('78) showed, is quite variable. Passing over the work of Angelucci ('78), who reported definite pigment movements in the rabbit, there remains Chiarini's ('06) description of the slight differences observed in the retinas of dogs which were exposed to direct sunlight and to darkness. The pigment of the light-adapted animals extended in short fringe-like processes between the rods, in contrast to the densely contracted pigment of the reciprocal set. Finally, Garten ('07) carried out carefully executed experiments on the ape, ox, rabbit and rat, yet failed to observe any striking differences between the effects of light and darkness.

However, in the retina of the ape, which has a minute amount of pigment composed of needle-shaped granules, the pigment was extended 3 to 4 granules deep in the light and only 2 to 3 granules deep in the dark.

In summarizing the foregoing results concerning the effect of light upon the retinal pigment, it can be said that the most extensive migrations are found in fishes and in anuran amphibians, whereas the positional changes in the pigment of urodeles are relatively limited. Clearly defined movements of the retinal pigment also occur in both day- and night-birds. Although among reptiles and mammals the evidence is conflicting, it is probable that in some cases slight changes have been detected.

The first observation of the action of light on the cone cell was reported by Angelucci ('82), who maintained that a shortening and thickening of the outer member (cf. figs. 3 and 4, *prs. dist. con.*) was produced by an exposure of the frog's retina to light. This he still supported in later papers ('90), ('05), although Chiarini ('04 b) has suggested that a passive swelling probably occurred and Garten ('07) also failed to corroborate Angelucci's results.

The positional changes of the inner member of the cone cell through the action of light, was observed in 1884 by Stort, a student of Englemann, and the first announcement was published by the latter ('85). To the contractile portion of the inner member, between the external limiting membrane and the ellipsoid, Englemann gave the significant name of myoid (cf. figs. 3 and 4, *my. con.*). In some fishes a shortening of the myoid to ten per cent of the length which it assumes in darkness occurs through the action of light. If effective at all, light causes a shortening, and darkness a lengthening in the cone myoids of all vertebrates (figs. 3 and 4).

Stort ('87) extended his first discovery on the frog by experimentation upon representatives of the other vertebrate classes. He reported that a similar condition existed in the cones of Perca, Triton, Columba, and Sus. His measurements of one dark-adapted human eye do not, however, prove that movements of the cones occur in man.

The most noticeable positional changes are found in fishes, among which, however, the eel is exceptional, for Garten ('07) was unable to discover perceptible differences, although the rods and pigment exhibited striking movements.

Among amphibians, the small cones of the frog (Stort) and of the toad (Arcoleo, '90) give clearly defined responses when stimulated by light. Movements of the cones of the salamander were likewise described by Angelucci ('90), but this was not supported by Garten's ('07) observations.

It is a matter of some theoretical importance to determine whether there is any correlation between the extent of movement of the cones and the ratio expressing the frequency of rods to the cones in various regions of the same retina or in retinas of different animals. In the rodless retina of Tropidonotus natrix, Englemann ('85) found but very limited changes in the length of the cone myoids, while in Testudo graeca, which also presumably has no rods, the evidence for movement was extremely doubtful. Angelucci ('90), however, insisted that light affects the cones of Testudo marina, although to a less extent than it does those of the frog. The changes in the rodless retinas of the lizard and the chamaeleon are also slight, as Chiarini ('06) and Garten ('07) respectively observed.

In the retina of birds it is possible to compare the movements of the cones in regions which have many rods, few rods, and none at all, these regions being respectively known as the yellow field, red field, and fovea. The relative change in length, as measured from Stort's ('87) plates of the pigeon 's cones, can be expressed as follows:

$$\text{fovea: red field: yellow field} = 23 : 32 : 40.$$

Garten ('07) substantiated this relation between the amount of movement in the fovea and yellow field of the pigeon and extended his observations to the owl and the hen. Contrary to many earlier statements, the retina of the owl has been shown to possess exceedingly delicate cones whose movements are more extensive than are those of the pigeon. The rods of the hen's retina are sparse and changes in the positions of the cones apparently do not occur.

Among mammals, the results of Stort ('87) stand alone in ascribing striking positional changes to the cones. This worker found the cone myoids of the pig to measure 5.7 μ in darkness and 2.3 μ in light. Chiarini ('06) obtained negative results on the dog's eye, although Garten ('07) working on apes, in a series of careful experiments, has been able to demonstrate slight changes in the region of the fovea. Garten suggests the possibility of the changes in all the retinal elements of mammals occurring so quickly that the slowness of penetration of the fixing fluid fails to preserve them in an extended condition. The rapidity of movement is perhaps correlated with the rich blood supply which these retinas receive in contrast with the condition in the lower vertebrates. It is significant to note in this connection that the eel's retina, in which movements of the cones were not demonstrable, is the only one among the lower vertebrates which is supplied with blood vessels.

The more distal portion of the inner member of the cone cell, the ellipsoid (cf. figs. 3 and 4, *ell. con.*), has been recorded as changing its shape. Thus Stort ('87) observed that the ellipsoid of the frog was broader and shorter in the light, and conceived of the change as being of an entirely passive nature. Chiarini ('04 a) found the same condition and assumed that the lateral pressure of the rods on extended cones caused the elongation of the ellipsoid in the dark. Both of these views were in opposition to that of Angelucci ('90), according to whom the ellipsoid and outer member actively shared in causing the movements of the cones.

Hence it is seen that the greatest contractility of the cone myoid, through the action of light, is found in fishes, although well defined responses are also shown in the frog, toad, and in some birds, including one which is nocturnal in its habits. Among reptiles and mammals, changes in the length of the cone myoid are very difficult to observe, yet in both groups, responses to light have apparently been detected in a few instances. Changes in the outer member and in the ellipsoid of the vertebrate cone are presumably of a passive nature.

The visible response of the vertebrate rod to the action of light is not identical throughout the various classes. Among

amphibians a slight shortening of the inner member probably occurs, whereas in fishes (figs. 3 and 4, *my. bac.*), and birds there is a marked elongation.

After strong illumination, Ewald und Kühne ('78) first observed a change in the outer member (cf. figs. 3 and 4, *prs. dst. bac.*) of the frog's rod, in which a thickening or swelling was said to take place. Angelucci ('84) measured the lengths of the rod's outer members and found that they were shorter in the light; later ('90) he confirmed this result by measurements of the large rods of the salamander, where the difference in length was more striking. Arcoleo ('90) and Garten ('07) reported similar conditions for the toad and the frog respectively.

The inner member of the frog's rod likewise shortens when exposed to light, as was recorded by Angelucci ('84) and Gradenigro ('85). Later, in 1890, Angelucci borrowed the term 'myoid' which Engelmann had given to the contractile portion of the cone's inner member and applied it to the corresponding part of the rod (figs. 3 and 4, *my. bac.*). Recently Lederer ('08) has challenged the result of the previously named workers. According to his statement the rods of the frog elongate in the light as do those of fishes and birds. Arcoleo ('90), on the other hand, using pithed toads, observed conditions similar to those reported by Angelucci and by Gradenigro, for he states that in the light the rod's inner member became 'broad and short.'

In connection with these conditions among amphibians should be mentioned the work of Stort ('87), who first asserted that in the dark the nuclei of the rods in Triton migrated partially through the external limiting membrane and thereby caused the whole rod to become extended, whereas in the light these nuclei lay completely within the outer nuclear layer. The contractility of that portion of the rod cell between the rod nucleus and the external molecular layer was believed to cause these movements. Angelucci ('90) made similar observations on the salamander. These conclusions relative to positional changes were preceded by the earlier observations of Czerny ('67) and especially of Gradenigro ('85), who merely recorded changes of form in the nuclei of the external nuclear layer.

Among certain other animals, however, the response of the rod myoid to light unquestionably consists in an elongation (figs. 3 and 4). Stort ('86) first showed the movements of the rods of the crow to be more extensive than the limited changes in amphibians. In dark-adapted retinas the rods were much retracted, while in the light they were extended toward the choroid, and the inner members, which previously had been thick, were now tenuous.

H. Müller ('57), long before, had observed this higher position which the inner member of rod cells occasionally assumed and since the action of light on these elements was at that time unknown, he believed it to be due to faulty preservation.

Garten ('07) confirmed the results of Stort on the crow and the pigeon and extended the work to include the rods of the hen. In an owl (Syrnium aluco) as a type of nocturnal bird he could discover no significant changes.

Among the fishes Stort ('87, p. 344) also recorded that in the light, "la limite des segments externe et interne est située beaucoup plus haut que chez la perche à l'obscurité," yet this statement for a long time remained unnoticed. Pergens ('96) was not able to demonstrate satisfactorily the fine rods of Leuciscus, yet he assumed, although wrongly, that their movements corresponded to those of the cones. Chiarini ('04a), with good fixation, found no significant changes in the position of the rods of Leuciscus and further ('06) denied the occurrence of movement in the rods of all vertebrates. Garten ('07), however, states positively that elongation of the rods of Leuciscus does occur in the light, as it certainly does in many other fishes that have since been investigated (figs. 3 and 4). Garten further showed that in the eel, the rods undergo movements, although the cones do not, and accordingly these changes in the rods can not be passively brought about through the movements of the cones. No movements, however, were observed in the rods of Scyllium and Torpedo—the retinas of these fishes lacking cones. In general, it may be safely asserted that there are positional changes as a response to light in the rods of all fishes which possess cones.

The responses of all vertebrate rods to light, therefore, are not identical. The outer members of amphibian rods appear to shorten and thicken through the action of light, but there is a diversity of opinion as to whether or not the myoids do the same. In the dark, the nuclei of the rod cells of urodeles move toward the choroid and may in this way change the position of the rod proper; the myoid, however, is said not to participate in causing this movement. In all fishes that possess cones there occurs an extreme lengthening of the rod myoid in the light, and a shortening in the dark; similar responses have been found in certain birds having diurnal habits. No experimentation has been performed upon the rod cells of mammals or of reptiles, although in the latter group, the retinas usually lack these elements.

Whenever a system of relations between an organism and its environment, and especially those involving constant responses to definite stimuli, is discovered, the theorist immediately busies himself in devising an explanation which will demonstrate the so-called adaptiveness of these relations. Although it is doubtless true that many such explanations reveal the resourcefulness of the human mind rather than the ingenuity of nature, yet a suggestive and stimulating hypothesis serves its purpose if only the possible dynamic interrelations of parts are thereby brought to light. Having completed, therefore, a summarization of the changes in the retinal elements which are produced by light, the question, What is the adaptive significance of these movements?, may now be fairly raised.

The significance of the movements of the visual cells and retinal pigment through the action of light has been sought by approaching the facts from various standpoints; inclusive explanations, however, are not easily devised, due to the lack of uniformity in the responses throughout the various vertebrate classes.[3]

[3] It is interesting to note that from the first discovery of a striking pigment migration in the frog's retina a similar condition was assumed for man. Misconceptions as to the amount of retinal pigment present in mammals and in man, and especially concerning the extent of its movement (e.g., Bailey, '13; Cunningham, '13), appear repeatedly in the literature of retinal physiology. One

Kühne ('78) expressed the belief that the chemical products formed by the decomposition of retinal pigment through the action of light served to stimulate the visual cells sufficiently to cause the sensation of vision. Besides the visual purple and brown pigment ('Fuscin') further 'Sehstoffe' were postulated in order to explain such cases as albinism. When one reflects upon the minute amount of substance that can produce the sensation of smell, it appears very probable that cells as highly specialized as the rods and cones, if open to chemical stimulation of this kind, could find their adequate stimulus in some such way as Kühne suggested. The anatomical isolation of the rod and cone layer from blood vessels would also retard the removal of decomposition products and allow them to become effective. Essentially similar views have been advanced by Boll ('81) and Gad ('94). At its best, however, this theory has many objections and it is doubtful if the retinal pigment acts in this way.

A relation between the retinal pigment and the regeneration of visual purple was maintained by Ayres and Kühne ('78), who directly compared the pigment cell to a gland, the secretion of which is the visual purple. This conception was supported by experiments, among which the use of pilocarpin was found to reduce greatly the time of visual purple regeneration in the dog and rabbit; the similar effect of this drug upon the activity of glandular epithelium in general is well known. Dreser ('86) corroborated, on the frog, these results. Kühne ('79) cites the parallelism between the time needed for the regeneration of visual purple in the frog and the length of time in which dark adaption is first accomplished, as evidence of a significant relationship existing between the two. In mammals with their minute amount of retinal pigment, which undergoes but limited migration if any at all, these relations with the visual purple are not evident and a more inclusive explanation is demanded. This was furnished

of the more recent examples is found in the elaborate theory of the significance of pigment migration advanced by Klein ('11), who assumes, on subjective grounds, the existence of extensive movements of the human retinal pigment. In a similar way subjective observations have lead other writers to take for granted that the cone cells of man likewise undergo striking positional changes.

by Garten ('07), who suggested the possibility that the basal part of the pigment cell (figs. 1 and 2, *pd. cl. pig.*) is concerned in all activities heretofore ascribed to the pigment, whereas the movement of the pigment in the processes has an entirely different significance.

The expansion of pigment in the retina of the frog was considered by Herzog ('05) to be of use in storing up radiant energy, in the sense that the dark heat waves thus made available would accelerate the chemical processes taking place in the photoreceptors.

Chiarini ('06) believed that the function of the migrated pigment is nutritive, the rods and cones thereby being recompensed for the losses which they incur during functional activity. The pigment was also supposed to protect the visual cells from overstimulation by light.

It has been suggested that the expanded pigment surrounding the outer members of the visual cells serves to absorb all light which escapes from the rods by refraction and thereby makes possible an independent stimulation of the individual cells. Garten ('07) investigated this experimentally and showed that light, entering the rods of mammals (these elements not being surrounded by pigment), underwent total reflection, while in lower vertebrates the refraction was such that light did escape from the outer members of the rods and was presumably kept from entering adjacent rods by being absorbed in the expanded pigment.

These latter results are very suggestive since the conclusion drawn by Garten possesses the merit of having been based upon actual observation. It would be interesting to ascertain whether this correlation between pigment migration and the refractive index of the rod's outer member extends throughout all classes of vertebrates. Garten's data were obtained from several mammals and fishes, and from the frog; the crucial test, however, would consist in determining the indices of refraction of the rods in the pigment-free retinas of certain elasmobranchs, in the retinas of urodele amphibians, where both the amount of pigment

and the degree of migration is limited, and in the rather heavily pigmented retinas of birds.

The movements of the cone cells are of doubtful significance with respect to light perception. Angelucci ('90) naïvely supposed that the positional changes in the visual and pigment cells directly induced the sensation of light. This view has been sharply criticized since it fails signally to account for many commonplace facts of retinal physiology. The slowness of the reactions, the equal responses of the elements to colored lights, the absence of movements among mammals and the changes induced by stimulating agents other than light which do not produce the sensation of light, are the more important objections that have been advanced.

Herzog ('05) and Exner und Januschke ('06) have developed the theory that in dim light, when rod vision occurs in the sense which Max Schultze uses the term, the cones are elongated in order that the rods may fully utilize the light rays which enter the eye.[4] It must be assumed in such a theory that the cone cells remain elongated in very dim light. This, however, as Garten and Weiss showed on Abramis, is not true, and accordingly the whole theory is fundamentally undermined.[5]

Granting that the movements of the retinal elements may have a significance in the physiology of light perception, the nature of which is yet quite obscure, I nevertheless believe that from the extent of our present knowledge the responses of these elements can only be interpreted in terms of the action of definite stimulating agents upon protoplasmic cells. The acceptance of such a conservative attitude does not entail the abandonment of theoretical suggestions provided they are based on sound

[4] In the same way, the elongation of the numerous small rods of fishes and birds in the light, might be interpreted as a response which serves to remove the rod cells from the immediate vicinity of the retracted cones and thereby allows more direct illumination of the latter. However this may be, it is certain that in the highest vertebrates, where vision is best developed, the movements of the visual cells are very slight, if indeed they occur at all.

[5] If the rods of fishes and birds were also shown to move (elongate) in dim light, resulting in their removal far above the external limiting membrane, the last support of this theory would be destroyed.

experimentation—a course that has hitherto been followed in only a few instances. Inclusive theories, devised at the writing desk, can hardly be expected to offer rational explanations of such phenomena as are involved in the diversified responses of the retinal elements.

The retinal pigment cell is very comparable to a melanophore and the positive phototropism of its granules is quite likely a mere retention of a primitive response, for as Parker ('06, p. 413) asserted: "It is probable that in all melanophores (*sensu lato*) in which there is a migration of pigment, light . . . . will induce a migration toward the source of illumination and the absence of light . . . . a migration in the reverse direction."[6]

Reviewing the conditions in the several vertebrate classes, a high degree of variability appears. In most fishes the migration of pigment is extensive, although in certain common elasmobranchs pigment is entirely absent. Among amphibians there are wide differences. In the frog, the movements are extensive but are highly specialized, since it is probable that in many cases, e.g., reactions to temperature (Herzog '05), a nervous control has been superimposed over the primitive direct responses. Of the urodeles, Necturus shows a very limited capacity, and Triton a comparatively well developed capacity for executing positional changes of the pigment. In reptiles and mammals movements are demonstrated only with difficulty, yet among birds extensive migration again appears.

The discontinuity of the pigment response throughout these classes, and the variability in the degree of pigmentation as well

[6] This statement as it stands is not true for a few special cases. Steinach ('91) on the eel and Hertel ('07) on Triton found that a blanching of the skin (pigment contraction) resulted from an exposure to the light, and also, as Harless ('54) first showed, the skin of the frog becomes dark in darkness but brightens in the light. Moreover, it is doubtful whether the movement of the pigment granules in all melanophores that do expand in the light and contract in darkness is respectively toward and away from the source of illumination. In melanophores of fishes the direction of movement appears to be nearly lateral, whereas in the frog there is, to be sure, a vertical component of movement, yet in the light this migration is away from the source of illumination and in darkness in the reverse direction. The influence of the nervous system, which plays an important rôle in the behavior of melanophores, undoubtedly complicates the primitive responses in many animals.

make it probable that evolution has worked in different ways with these cells, some remaining much more strongly developed than have others, but through it all there has been a retention, to a greater or less degree, of the primtive phototropic response. Assuming that pigment migration, when present, may have a significant relation to the mechanism causing light perception, it is evident that animals, in which positional changes of the pigment are absent, must have produced a compensatory adjustment in another way.

The movements of the visual cells likewise show certain inconsistencies. In all vertebrates whose cones are capable of movement, a shortening occurs in the light. The rods, on the contrary, are not as uniform in their responses, since among amphibians light presumably causes a slight shortening, whereas in fishes and birds a striking elongation takes place. If the responses of the visual cells to light are adaptive, there must be a wide difference in the uses to which the elongation of rods in some animals and the shortening in others is put. The mere statement that the cone myoids shorten in the light in order to make better use of the available light energy leaves unanswered the other half of the question involving the significance of elongation in the dark, for, as was previously stated, the cones remain shortened in twilight and hence elongation of these elements is not obviously related to the phenomenon of rod vision.

In a forthcoming paper by the writer, which will include a discussion of certain aspects of the discrepant responses of the retinal elements, it will also be shown that the temperature reactions of the visual cells and of the retinal pigment throughout the various vertebrate classes likewise are inconsistent and therefore presumably have no common adaptive significance.

In reviewing the present status of our information concerning the movements of the visual cells and retinal pigment, therefore, the general conclusion seems justified, that although the movements of these elements, when present, may have a certain unknown significance in connection with the mechanism of light perception, we can at present interpret such movements only in terms of protoplasmic responses to definite stimulating agents.

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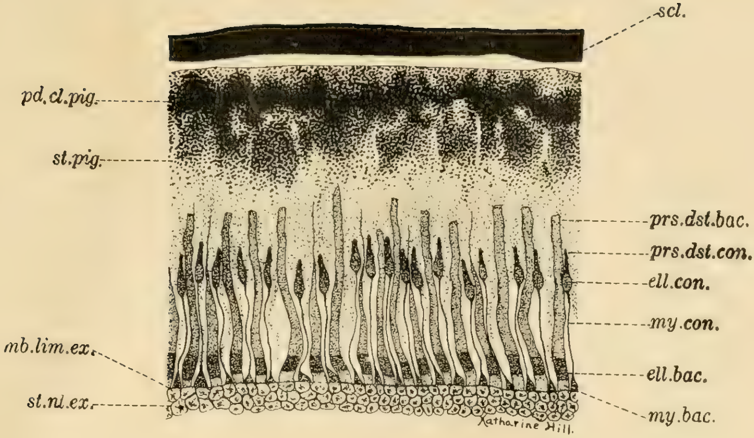

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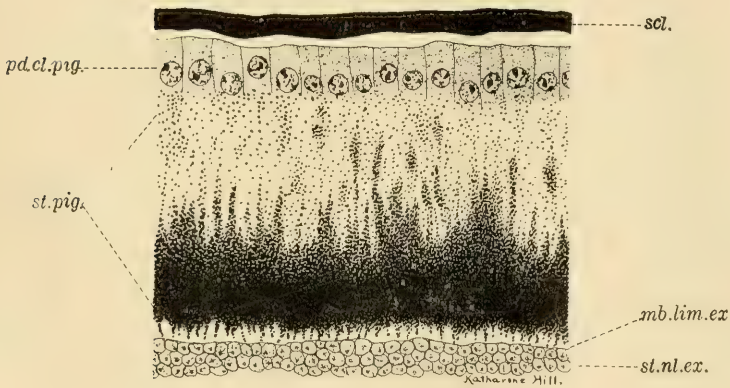

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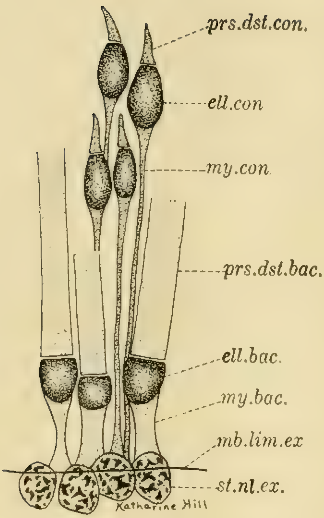
Fig. 1 Showing the distribution of the retinal pigment of the common horned pout, Ameiurus nebulosus, in darkness (× 160). The rod and cone cells are entirely free from pigment and are, therefore, easily demonstrable.

Fig. 2 Showing the distribution assumed by the retinal pigment of Ameiurus in the light (× 160). The expanded pigment accumulates near the external limiting membrane, thereby masking the visual cells.

ABBREVIATIONS

ell.bac., rod ellipsoid
ell.con., cone ellipsoid
mb.lim.ex., external limiting membrane
my.bac., rod myoid
my.con., cone myoid
pd.cl.pig., base of pigment cell
prs.dst.bac., outer member of rod
prs.dst.con., outer member of cone
scl., sclera
st.nl.ex., outer nuclear layer
st.pig., pigment layer



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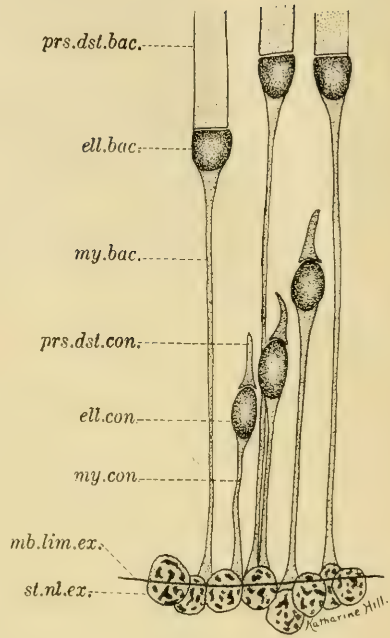

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Fig. 3 From the dark-adapted retina of the common horned pout, Ameiurus nebulosus, showing the positions assumed by the rod and cone cells (× 930).

Fig. 4 From the light-adapted retina of Ameiurus, showing the positions assumed by the visual cells (× 930). The change in the length of the cone myoid is not as striking in Ameiurus as it is in most fishes—in the shiner, Abramis crysoleucas, for example, the cone myoid shortens in light to 10 per cent of its length in darkness. The change in the rod myoid, on the contrary, is especially well marked in Ameiurus, the maximum ratio of its length in darkness and in light being 1:10.

ABBREVIATIONS

ell.bac., rod ellipsoid
ell.con., cone ellipsoid
mb.lim.ex., external limiting membrane
my.bac., rod myoid
my.con., cone myoid
prs.dst.bac., outer member of rod
prs.dst.con., outer member of cone
scl., sclera
st.nl.ex., outer nuclear layer

ON THE BRAIN WEIGHTS OF RATS DESCENDED FROM THE CROSS BETWEEN THE WILD NORWAY (MUS NORVEGICUS) AND THE DOMESTICATED ALBINO (MUS NORVEGICUS ALBINUS)

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TWO CHARTS

The present study was undertaken to determine the influence of the parental brain weight on that in the offspring. For this purpose wild norway rats (Mus norvegicus) were crossed with their domesticated variety, the albino rats. The main advantages in employing these animals are two: 1) these two forms interbreed readily in confinement (Hatai, '07) and 2) the brain weight in the Norway is considerably heavier (about 14 per cent in the adults) than that of the Albino of the same body weight or length (Donaldson and Hatai, '11). It was thought possible that the respective brain weights might be inherited as Mendelian characters and thus enable us to differentiate the Norway type from the albino type among the descendants. At the same time we encounter in such a study several drawbacks: 1) the fact that we do not possess any data by which to estimate the probable effect of domestication on the Norway rats during the experiment and 2) that we do not know the effect of close inbreeding on the weight of the brain under the changed conditions for the Norway.

The lack of these data naturally limits our interpretation of the results. Nevertheless the results thus far obtained seem to indicate rather clearly that the brain weights in the hybrids lie practically midway between those in the parents. Thus the inheritance of brain weight in this experiment appears to be an example of 'blending inheritance' and it is the object of the present paper to give the evidence for this conclusion.

MATERIAL

The Norway rats here used were trapped at different points in the city of Philadelphia, while the Albinos were secured from the colony kept at The Wistar Institute. The total number of the Norway rats employed was 6 males and 4 females, and of the Albinos used, 3 were males and 9 females. With these rats 14 matings were made successfully. Although more than twice the number of rats named above were mated at the beginning of the experiment, the data for many had to be discarded on account either of the loss of parents or of the sterility of the hybrids of the F_1 generation. Only those cases in which the data on the parents as well as their offspring for the first two generations were secured, were used in the present paper. The total number of the hybrids examined was 110 F_1 and 149 F_2.

THE METHOD OF COMPARING THE BRAIN WEIGHTS

In comparing the brain weights in the hybrids with those in the parents, the following method was adopted. As has been already found by Donaldson ('08) with the albino rat, and by Donaldson and Hatai ('11) with the Norway rats, the brain weight varies with the body length according to a logarithmic law. Since the body lengths in the hybrids were not identical with those in the parents, a direct comparison of the observed brain weights without a due consideration of the difference in the body length was not justified. The proper adjustment was however made possible by utilizing the following formulas (for sexes combined).

For Norway rat (Donaldson and Hatai, '11).

$$\textit{Body weight} = 10^{\frac{\textit{Body length} + 165}{159}} - 18$$

$$\textit{Brain weight} = 0.825 \log (\textit{Body weight} - 4) + 0.233$$

For albino rat (Donaldson, '08)

$$\textit{Body weight} = 10^{\frac{\textit{Body length} + 134}{143}} - 15$$

$$\textit{Brain weight} = 0.569 \log (\textit{Body weight} - 8.7) + 0.554$$

The frequency distribution of the brain weights within the litter seems to be continuous, and thus the Norway type or albino type cannot readily be differentiated. Consequently I have adopted the statistical method of taking the averages of all the rats belonging to each generation separately. At the same time I have plotted all individual brain weights in chart I in order to show the extent of the variation, as well as the relative positions held by the records belonging to the different generations.

The averages were taken for the sexes combined. This procedure affords some advantage since by this means we can deal with a larger number of rats and thus can eliminate irregularities arising from the averages of smaller data. Any disturbance which arises from the sexual difference in the brain weights is almost insignificant since such a difference amounts to less than 0.5 per cent in the albinos and about 1 per cent in the Norway rats. The formulas given above may be applied directly when the sexes are not distinguished.

BRAIN WEIGHTS IN THE NORWAY AND ALBINO RATS

In table I are given the data on the brain weights for both the norway and albino rats which have been used as parents of F_1 in the present experiment. As will be seen some rats are recorded in the table several times. This repetition was necessitated by the fact that these rats were crossed several times with different rats and thus they were counted as often as the matings were made.

Norway rat. The observed average brain weight of the Norway rats with a body length of 237 mm. is 2.251 grams. According to the formula the Norway rat with a body length of 237 mm. should give a brain weight of 2.295 grams. Thus the observed brain weight is 1.91 per cent less than the value given by the formula. The computed brain weights for the Norways which appear in chart I were obtained by subtracting 1.91 per cent from the formula values.

Albino rat. In the albino rat with a body length of 194 mm. we obtain an observed average brain weight of 1.740 grams. The formula gives however 1.827 grams for the body length of 194 mm., thus the observed brain weight is 4.65 per cent less than the value given by the formula. The computed brain weights for the Albino which appear in chart I were obtained by subtracting 4.65 per cent from the values given by the formula. These computed values for the Norway and albino rats were taken as the basis for estimating the positions which the brain weights of the hybrids occupy.

TABLE 1

Showing the data on the body length and brain weights in both the norway and albino rat used as parents

Norway M. × albino F. = 9 cases
Norway F. × albino M. = 5 cases

	Norway rats			*Albino rats*		
NO.	SEX	BODY LENGTH	BRAIN WEIGHT	SEX	BODY LENGTH	BRAIN WEIGHT
		mm.	*gms.*		*mm.*	*gms.*
b	M.	251	2.549	F.	190	1.596
c	F.	208	2.032	M.	205	1.807
j	F.	215	2.072	M.	209	1.937
o	M.	267	2.536	F.	180	1.702
A	F.	202	2.001	M.	208	1.827
AA	F.	214	2.199	M.	208	1.827
G	F.	200	1.925	M.	226	1.994
H_1	M.	255	2.337	F.	193	1.709
H_2	M.	255	2.337	F.	186	1.766
H_3	M.	255	2.337	F.	177	1.682
H_5	M.	255	2.337	F.	186	1.667
K	M.	260	2.342	F.	188	1.726
K_2	M.	260	2.342	F.	174	1.650
L	M.	223	2.172	F.	184	1.567
Averages		237	2.251		194	1.740
Calculated brain weight			2.295			1.827
Observed brain weight differs from computed by			−1.91 per cent			−4.65 per cent

BRAIN WEIGHTS IN THE FIRST HYBRID GENERATION RATS (F_1)

From the correlation table (table 2) the average brain weights corresponding to the different body lengths were calculated for F_1 and these are given in chart 1 together with the corresponding

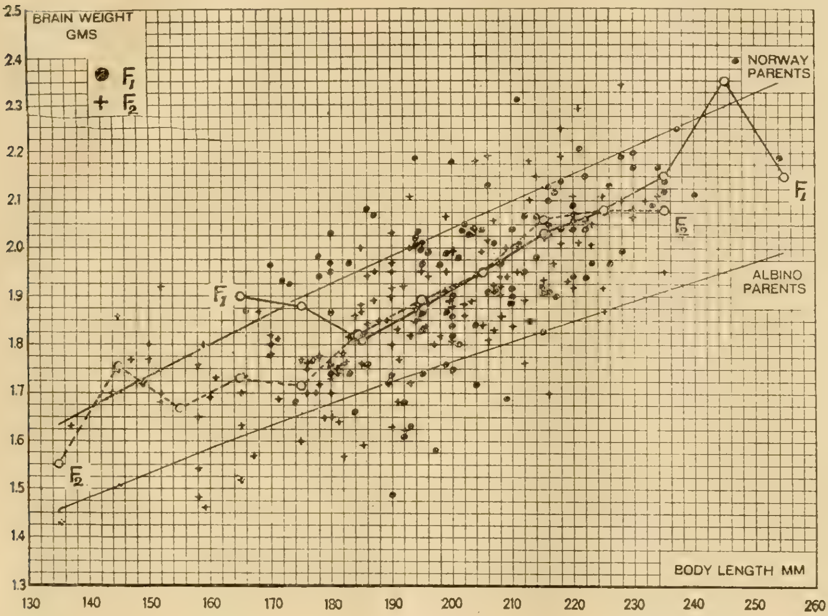

CHART 1

Showing the computed brain weights in the Norways and Albinos used as parents. Also the average brain weights for the F_1 and F_2 generations together with all the individual brain weights belonging to these hybrid rats.

———— Norway rat	———— Albino rat
○——○ F_1 hybrid	○ — — ○ F_2 hybrid
● F_1 hybrid	+ F_2 hybrid

individual brain weights. It is to be remembered that all the rats of this generation are gray in color. We note from the chart that with the exception of both ends of the graph where the number of observations is small, the average values give a very smooth graph and occupy practically intermediate positions between the brain weights given by the norway and albino parents. Furthermore, from the distribution of individual brain

weights (chart 1) we do not see any indication of discontinuity; in other words the distribution of the brain weights is concentrated round the average values instead of being concentrated about the Norway and Albino mean values respectively. This indicates that so far as the present data are concerned the brain weights in the first hybrid generation are intermediate between those of the parents. When the continuous character of the distribution of the brain weights is compared with calculated values according to the law of probability by the formula

$$y = 26.89\, e^{-0.1877\, x^2}$$

we note the close agreement between observation and calculation which justifies the statement made above. (Chart 2. F_1.)

TABLE 2

F_1 GENERATION	BRAIN WEIGHT GMS.										FREQUENCY BODY LENGTH	MEAN BRAIN WEIGHT
Body length	1.4–1.5	1.5–1.6	1.6–1.7	1.7–1.8	1.8–1.9	1.9–2.0	2.0–2.1	2.1–2.2	2.2–2.3	2.3–2.4		
mm												
160–170					1	1					2	1.90
170–180			1	2	2	5	1				11	1.88
180–190	1		1	3	1	1	2				9	1.81
190–200		1	3	3	7	5	4	2			25	1.88
200–210			1	2	3	5	7	1			19	1.95
210–220					3	6	11	3		1	24	2.03
220–230						4	2	5	1		12	2.08
230–240							1	4	1		6	2.15
240–250										1	1	2.35
250–260								1			1	2.15
Frequency brain weight........	1	1	6	10	17	27	28	16	2	2	110	

BRAIN WEIGHTS IN THE SECOND HYBRID GENERATION RATS (F_2)

In chart 1 the average brain weights for corresponding body length as well as the individual brain weights for F_2 are recorded. The averages were obtained from the correlation table (table 3). As is shown in the chart the average brain weights in the second hybrid generation are practically identical with those in the first

TABLE 3

F_2 GENERATION	BRAIN WEIGHT GMS.										FREQUENCY BODY LENGTH	MEAN BRAIN WEIGHT
Body length	1.4–1.5	1.5–1.6	1.6–1.7	1.7–1.8	1.8–1.9	1.9–2.0	2.0–2.1	2.1–2.2	2.2–2.3	2.3–2.4		
mm.												
130–140	1		1								2	1.55
140–150				6	1						7	1.76
150–160	2	1	3	2	1	1					10	1.67
160–170		2	1	5	3						11	1.73
170–180		1	4	9	1						15	1.72
180–190		2	2	8	8	7	1				28	1.82
190–200			2	2	11	8	2	1			26	1.89
200–210					8	7	3	2			20	1.95
210–220			1	1	1	5	2	5	1		16	2.06
220–230					1	1	6	1	1	1	11	2.08
230–240						1		2			3	2.08
Frequency brain weight........	3	6	14	33	35	30	14	11	2	1	149	......

hybrid generation and thus the brain weights occupy an intermediate position between the values given by the norway and albino rats and are like those of their immediate ancestors.

The distribution of the individual brain weights in F_2 rats is similar to that of the F_1 rats and the concentration is greatest round the mean value. The frequency distribution of the brain weights in F_2 rats is best shown in chart 2 where observed frequencies are compared with those computed by the following formula for the normal probability

$$y = 34.41\, e^{-0.1725\, x^2}$$

FREQUENCY CURVES

Particular interest attaches to the frequency curves (chart 2) given by the brain weights in both the F_1 and F_2 series. The observed frequency distribution is closely represented by the normal probability curve; that is the distribution is symmetrical around the mean brain weight. I have shown in a previous paper (Hatai, '11) that the symmetrical distribution of the

characters may arise when the two parental characters blend together with equal potency and the limiting case of such distribution leads to the normal probability curve. The brain weights here investigated may thus be taken as a good example of the limiting case of the formula of the blending inheritance, where dominance is absent.

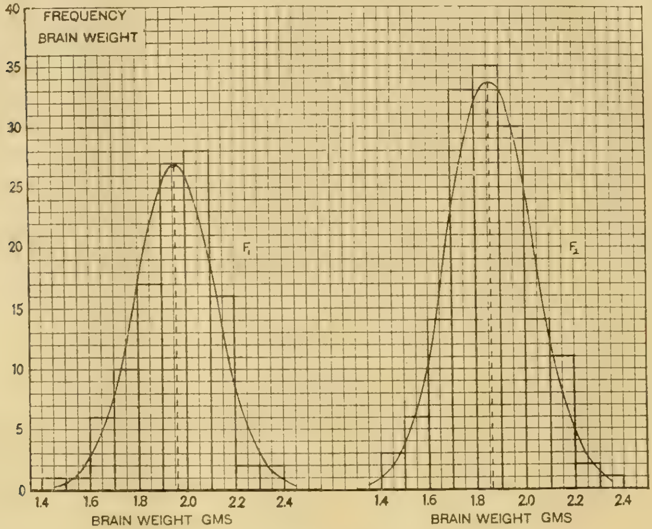

Chart 2

COAT COLOR AND BRAIN WEIGHT

It may be added that in the F_2 generation we usually obtain five varieties of coat color in rats; self gray, black, gray piebald, black piebald and albino (see Bateson, '09). In our experiment the mortality was somewhat large and in as much as the inheritance of the coat color was not the object of the present experiment, the census of the coat colors of the dead rats was unfortunately not taken. We find however from an examination of the final records 42 albino and 107 pigmented rats, or a proportion of 1 albino to 2.6 pigmented, thus coming very close

to the expected number of one Albino to three pigmented. I have tried to determine whether or not the brain weight varies systematically with coat color. The following table gives the results of examination.

	BODY LENGTH	BRAIN WEIGHT	CALCULATED BRAIN WEIGHTS INTERMEDIATE BETWEEN PARENT NORWAY AND PARENT ALBINO	DEVIATION FROM CALCULATED INTERMEDIATE VALUES
	mm.	*gms.*		*per cent*
Pigmented coat.	186	1.854	1.896	−2
White...........	195	1.860	1.947	−4

So far as the tabular values are concerned, the hybrids with pigmented coats give slightly heavier brain weights than those with non-pigmented coats. However owing to a somewhat greater mortality among the pigmented rats, it is possible that those which died previous to the examination might have been physically inferior individuals which possessed smaller brains. Even as it stands the difference of 2 per cent is certainly not high enough to be significant when the great individual variability in the brain weights in these hybrids is taken into account. I am thus inclined to believe that there is no definite correlation between the brain weights and the characters of the coat under these conditions.

REMARKS

As has been stated, the brain weight character appears to blend in inheritance. In this respect the brain weight behaves like body size—weight and length—as well as such characters as ear length and skeletal dimensions in the rabbits studied by Castle and his collaborators ('09).

It has been found by several investigators that in many cases of blended inheritance the characters under consideration show a greater degree of variability in the second filial generation (F_2) than in the first filial generation (F_1). This greater variability in the F_2 has been regarded by a number of investigators (see

Castle, '11) as an indication of the segregation of the character without dominance. My own data are not sufficient for the full discussion of this question and furthermore the material itself is not ideal for the purpose, owing to the probable influence of domestication on the Norway factor. However, so far as my present data show, the degree of variability in the first and second filial generations is practically identical. We find the coefficient of variation of brain weight for F_1 to be 8.603 ± 0.396 while that for F_2 is 8.774 ± 0.343.

It is desirable in this connection to state clearly the difficulties which at present prevent us from reaching a definite conclusion. These difficulties are the following:

a) The wild Norway rats when kept under captivity are furnished with a presumably unaccustomed diet. Since in many animals domestication apparently alters the normal relation between the body size and brain weight (see Darwin, '83 and Lapicque and Girard, '07) the probable effect of captivity on the Norway rats as to their brain weights should be taken into consideration. If the Norways were thus losing in relative brain weight the influence of the Norway factor might be diminished.

b) The brain weight varies with the body size in the rats (see Donaldson, '08, and Donaldson and Hatai, '11). It is therefore possible that any factors which alter the normal growth of the body size may also alter the relative brain weights or even the brain weights may suffer quite independently of the body size.

In spite of these possible sources of error it is to be noted first that the mean brain weights in the F_1 and F_2 generations are well above those for the albino parents, showing that some factor was at work to raise the brain weight above that characteristic for the Albinos, and that there is no trace of segregation in the F_2 generation.

The above statements have been added here to show the possible precautions to be observed while interpreting the results given in the present paper.

I am however confident that the rats examined here were free from all gross abnormalities and furthermore it is my impression

that, provided the dietary factor was properly adjusted to the animal, the Norway rats may not have suffered any considerable physical alteration during the short period of captivity (two years or more).

One peculiar phenomenon appearing in the present study was that the range of variability in the brain weights for any given body length was noticeably greater in the hybrids than when either the Norway or albino rats alone were treated. Whether this wide range of brain weight distribution is characteristic for the hybrids in general, or whether it was due to the effects of captivity (including the dietary factor) on normal growth of the brain in weight is difficult to decide. We must await further observations.

CONCLUSIONS

Despite the fact of the several difficulties already mentioned we may draw the following conclusions:

1) The hybrid offspring F_1 and F_2 from Norways $\times$ Albinos possess brain weights which are intermediate between the brain weights given by the norway and albino parents respectively.

2) The frequency distribution of the brain weights in F_1 and F_2 is symmetrical round the mean brain weight, and is closely represented by the normal probability curve. There is no evidence of segregation.

3) It appears that there is no definite correlation between the size of the brain and the character of coat color; that is, the pigmented hybrid rats possess brain weights similar to those of the non-pigmented hybrid rats.

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SUBJECT AND AUTHOR INDEX